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PHYLETIC SIZE INCREASE, AN IMPORTANT TREND ILLUSTRATED BY FOSSIL INVERTEBRATES

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INTRODUCTION

One of the crowning achievements of paleontology, and of surpassing importance in the development of evolutionary theory, has been the discovery of innumerable graded morphological series of fossils showing progressive change as we ascend the geological scale of time. Many of the evolutionary modifications follow simple patterns, or trends, which recur again and again in related, or even unrelated stocks. One of the most prevalent, and perhaps the most important of all the trends among invertebrates—increase in mean size during evolution—is the subject of the present discussion.

Long ago Cope showed that there is a persistent and widespread tendency for body size in animals to increase during their phylogeny (Cope, 1885, 1896). Although the principle was illustrated mainly by examples from mammals and dinosaurs, Cope (*op. cit.*), Depéret (1907), and Rensch (1943, 1947, 1948), among others, have shown that there is also a tendency for increase in size during the evolution of invertebrates. As a matter of fact Haldane and Huxley (1927, pp. 276–280) have concluded that there has been an increase in mean size accompanied by increased structural complexity in large sections of the animal kingdom. This trend was known to Depéret (*op. cit.*) as the "law of phyletic increase in size" and Rensch (1948) terms it "Cope's law." For the purpose of this discussion the expression "phyletic growth" or "phyletic size increase" will be used.

In reviewing the history of any group of animals one is impressed by the fact that the largest known representatives are usually geologically younger than their smaller relatives. Furthermore, individual size commonly averages smaller when a group first appears than at any subsequent stage in its history. Among living forms are found the largest known representatives of the vertebrates, crustacea, echinoderms, pelecypods, gastropods, cephalopods, coelenterates, and annelids, and these are appreciably larger than the largest known fossil relatives. However, size increase is more characteristic of the evolution of some groups than of others, and is not, by any means, universal.

In some groups of Foraminifera (e.g. fusulines, nummulites) maximum size was attained at an intermediate period in their history and was followed by decrease in *mean* body size. Likewise the largest known representatives of the brachiopods (Mississippian), eurypterids (Silurian),

graptolites (Ordovician), trilobites (early Paleozoic), and insects (Pennsylvanian), among others, were outlived by smaller relatives. By the nature of the problem it is not at present possible to determine if this diminution is due to evolution from larger to smaller forms, or to elimination of the more robust lineages by extinction, without issue. In any case I am not acquainted with any well-documented evolutionary series among fossil invertebrates showing gradual mean size decrease over a considerable span of geologic time, but the converse situation is at least common.

There certainly is no indication, in the present state of knowledge, that phyletic growth leads to phylogerontism and "causes" racial extinction. For that matter, in light of the conclusions of the modern synthesis of evolution, there are no substantial grounds left for the theoretical concept of racial senescence.

Some great groups such as the radiolarians, brachiopods, bryozoans and graptolites show little or, at most, only a limited tendency for phyletic increase in the size of individuals. Generally, they have shown marked stability of size throughout geologic time.

Phyletic growth in animals is exceptionally important not only because it is common, and affects unlike groups, but even more so because evolution of diverse and seemingly unrelated characters is in many cases intimately related to changes in size. Evolution in some characters is, in a sense, *a consequence of increasing size*. Some of the apparently non-adaptive, so-called orthogenetic, trends undoubtedly are of this sort.

A number of investigators have shown conclusively that significant variation in the size of animals results in correlated allometric variation in form, structure, and even of function (e.g., C. Bergmann, 1847, 1852; D'Arcy Thompson, 1917, 1945; Julian Huxley, 1932; Rensch, 1947, 1948). According to Rensch, however, *the correlation between changes in body size and modifications in other characters need not be, and commonly is not perfect.* The evolutionary histories of many animal groups indicate that selection for gradual changes in body size is a common phenomenon. Size changes usually are accompanied by allometric alterations which in themselves probably are not always adaptive. As body proportions undergo allometric changes individual structures, at first non-adaptive, or only weakly affected by selection, may come increasingly under the influence of selection to the extent that they affect reproduction and survival. Therefore, "it appears . . . that natural selection controls not only body size as a whole, but also individual growth gradients" (Rensch, 1948, p. 219). This, of course, amounts to selection for the allometric relationship itself. Selection for change in an organ [1] having a given allometric pattern necessarily will change that pattern.

Those of us who had seen in phyletic allometry, or *allomorphosis*, as it is termed by Huxley, Needham and Lerner (1945), an early solution of the problem of apparently non-adaptive trends are given pause by Rensch's conclusion that "large species are not merely allometric alterations of related smaller species" (Rensch, *op. cit.*, p. 219). Where the interrelations between an evolving organ and changing body size conform to the allometric formula $y = bx^k$ it seems probable that commonly there is a common control. That is, changes in the organ clearly are related to and, in a sense, dependent on changes in body size. The relation between body and organ size need not always be a simple one, however, and differential growth ratios commonly do vary from the allometric formula in both ontogeny and phylogeny.

I am indebted to G. G. Simpson (personal communication) for pointing out that conformance to $y = bx^k$ in a differential growth relationship may, in particular cases, clearly be the result of selection. For example, increasing size mechanically demands changes that must be produced

[1] While it is perfectly true that selection operates directly on whole organisms, and only indirectly on separate organs, it is often convenient to discuss the effects of selection on single organs as though the action were direct.

by mutation and selection. As land vertebrates become larger their limb bones must become relatively (as well as absolutely) more massive, because body weight increases as the cube, bone strength as the square of linear increase. The curve produced by plotting diameter of limb bone against linear dimensions of the body is like that of an allometric curve, with a tendency for $k = 1.5$. Large animals without a proper relation between limb and body size would not survive. Increasing size in some cases permits desirable changes for increased efficiency impossible at smaller size. For example, a large brain can have more cells and nerve connections than a smaller brain, resulting in advantages which undoubtedly affect survival.

It appears, then, that the linearity of a trend may be due to two separate factors, operating simultaneously: (1) ortho-selection, and (2) allomorphosis resulting from changes in body size during evolution. Probably most allomorphic trends are so modified by selection that they do not conform to simple allometric patterns. Herein lies the real justification for employing the special term "allomorphosis" for evolutionary allometry.

Phyletic increase in size is of interest in another way. It is precisely in those groups which are most commonly affected by this trend (e.g., Foraminifera, corals, Mollusca) that ontogenetic development tends to parallel phylogeny. This, indeed, is a sort of recapitulation, although probably not in the sense of Haeckel. Critical reviews of the subject by Garstang (1922) and de Beer (1940), among others, show beyond reasonable doubt that recapitulation of ancestral adult characters in the original chronological order is a rare phenomenon and generally is more apparent than real. It is established that many characters which appear somewhere in the ontogeny of the ancestor commonly reappear in the ontogeny of the descendant, either at a corresponding stage of development, or earlier, or later, but this is not recapitulation as usually understood.

According to the classical theory of recapitulation, newly introduced heritable characters first appear in the mature stage of ontogeny. This additive phenomenon in evolution has been termed *hypermorphosis* by de Beer (1940, p. 65), who shows that this is only a special case among several possibilities. Evolutionary novelties may make their first appearance during any growth stage, and probably they are introduced as frequently in early or intermediate stages as later. De Beer (*op. cit.*) believes that phyletic size increase, because of the delay of the stage at which maturity is reached, relative to body growth, favors the terminal appearance of new characters in ontogeny, which leads to recapitulatory effects.

If, however, as frequently is the case in evolution, there is a gradual crowding of the growth sequence into the early stages (acceleration), phyletic increase in size may be inhibited, or even prevented by the "shrinking" of the earlier stages. It would seem that acceleration and phyletic growth are opposed phenomena.

Examples of Phyletic Growth

In the discussion which follows I shall briefly enumerate some examples of invertebrate lineages which illustrate phyletic increase in size. A possible correlation between various evolutionary trends and size increase is indicated and a limited explanation is suggested, based on selection for increasing size and resulting allomorphic effects.

Foraminifera

The individuals of a few families of the Foraminifera show well-defined size increase during evolution, up to hundreds of times the linear dimensions of the ancestors. The most celebrated examples are the fusulines of the late Paleozoic, and the nummulites and orbitoids of the early Tertiary. In these three groups and many others there is a marked increase in shell complexity in large forms as compared with smaller ancestors. There appears to be a close correlation between structure and size and it would, indeed, be

surprising if the elaboration of chambers and canals did not in some measure follow the allometric principle in phylogenetic development. Unfortunately, quantitative studies are not yet available on the subject. Repeatedly it has been suggested that the elaboration of the test in giant foraminifers is the result of selection for shell strength. Possibly this is true. In any case quantitative studies of these forms would indicate the extent to which shell complexity is due to allomorphosis correlated with increasing size.

The fusulines originated in lenticular coiled shells approximately 0.5 mm. or less in axial diameter (*Millerella*) during the late Mississippian and early Pennsylvanian (fig. 1, 1a). They gradually underwent change in form by a disproportionate lengthening of the axial dimension during increase in size through many species and genera, reaching an acme in microspheric giants (*Parafusulina kingorum* Dunbar and Skinner) 60 mm. long and 8 mm. in diameter. The more common megalospheric individuals of these large fusulines are of the order of 23 mm. in length. During some 40 or 50 million years the axis of coiling increased in length 45 to 120 times the primitive size.

Two general trends show some correlation with size increase. One of these is the tendency for progressive elongation in the direction of the axis of coiling, which gives the fusulines their characteristic spindle shape. In the largest and geologically youngest forms the test becomes almost cylindrical. The other conspicuous evolutionary trend is the progressive complication of septa of the shell. In the smaller and more primitive forms, the septa tend to be nearly flat. They are progressively modified by the appearance of undulations, which increase in amplitude and become highly symmetrical and complex in the geologically younger forms. It is, of course, a well-known fact that some comparatively large fusulines have relatively flatter septa than some of the more complex smaller ones. But within a given genus, or better, a given phyletic line, there is a marked correlation between intensity of septal fluting and size of the test, and it is quite possible that this correlation approximates the allometric formula.

Among the larger Foraminifera of the Tertiary there are several stocks which show progressive size increase. Near the close of the Cretaceous and beginning of the Tertiary period, several advanced Foraminifera gradually developed into phyletic lines of giants, the Orbitoididae, Nummulitidae, and Discocyclinidae, followed by the Miogypsinidae. The rapid differentiation within these families provides stratigraphers with some of the most valuable guide fossils. In all of these forms progressive size increase is accompanied by general increase in complexity of the organization of the test. Phyletic growth in the nummulites is accompanied by increasing compactness or tightness of coiling, and chambers tend to change from high and short to low and long. Davies (1935) has shown that small primitive nummulites have the form of lenticular disks. As they become larger during evolution, they may retain this shape or develop flat or globose forms. Ancestral forms in all lines have almost straight radial septal filaments (septal edges). With increasing size the septal filaments become wavy ("sigmoidal"), meandrine, or reticulate. The trend is toward a condition in which the septal filaments lose their individuality and become involved in a complex mesh (fig. 1, 2a–f). The most conspicuous change in size is seen in the range from early Paleocene forms which measure from a half to one millimeter in diameter to an acme in the middle Eocene in microspheric shells of *Nummulites* (fig. 1, 2f) which measure up to 120 mm. across the plane of the disk (*fide* Glaessner, 1947). The time involved in this change was of the order of 25 million years.

It may well be that in these groups of Foraminifera the most important trend in evolution has been the tendency for increasing size. If adequate quantitative studies reveal that increasing complexity of the test is correlated with increasing size

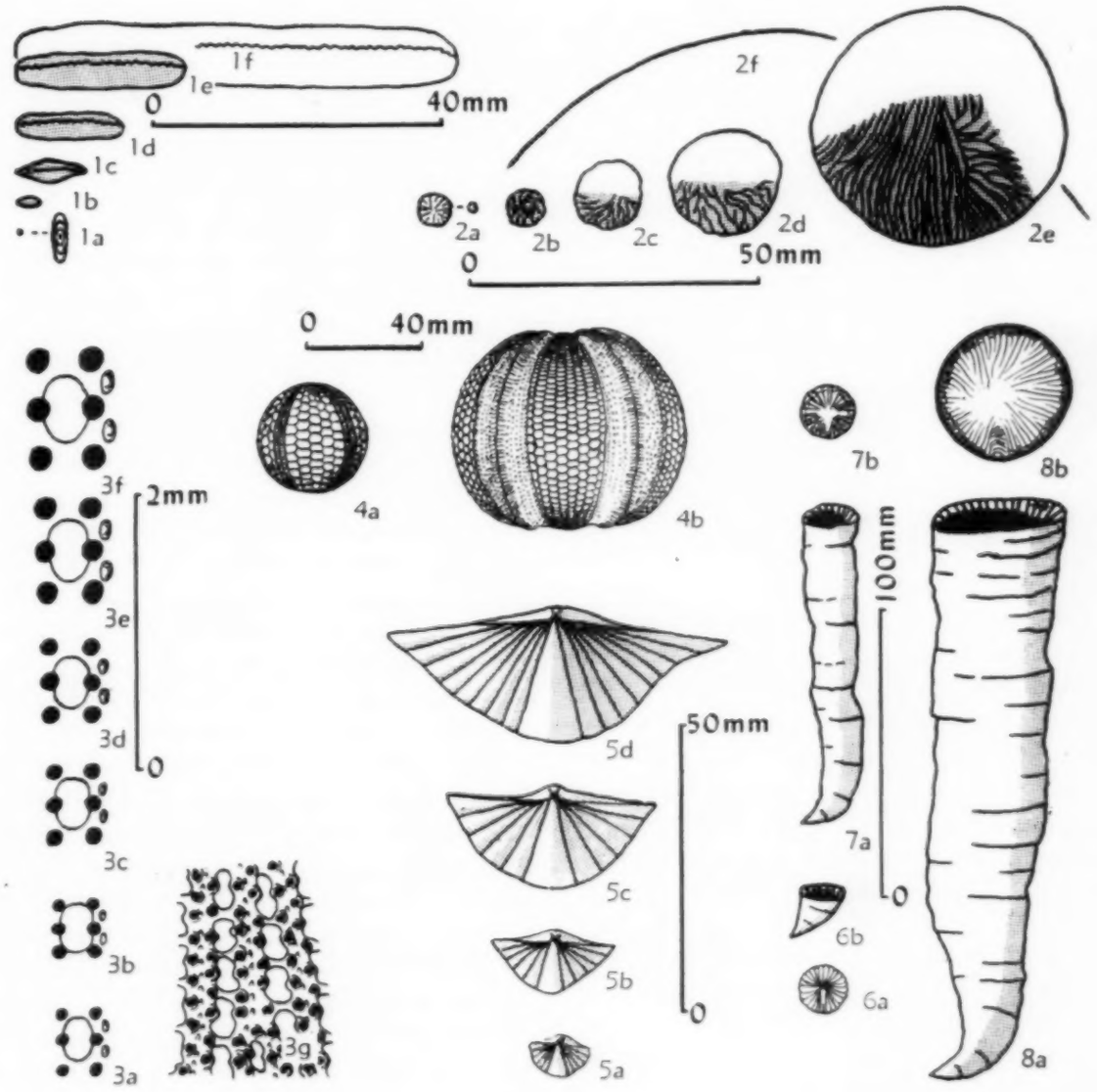

FIG. 1. Phyletic size increase in Foraminifera, Bryozoa, Echinoidea, Brachiopoda, and Anthozoa.

1a–f: Chronologic succession of late Paleozoic fusulines belonging respectively to the genera *Millerella, Fusulinella, Triticites, Schwagerina,* and *Parafusulina* (1e, megalospheric, 1f, microspheric *Parafusulina*), diagrammatic.

2a–f: Chronologic succession of early Tertiary species of *Nummulites* belonging to the species *N. deserti, N. globulus, N. planulatus, N. laevigatus, N. gizehensis* (2e, megalospheric, 2f, microspheric), diagrammatic.

3a–g: Chronologic succession of late Paleozoic species of the bryozoan *Fenestrellina. F. mimica latirama, F. mimica rogersi, F. mimica raymondi, F. mimica wellsi, F. parviuscula, F. girtyi, F.* sp. (data from Elias, 1937).

4a–b: Late Paleozoic Melonechinoida, *Palaeechinus elegans* and *Melonechinus multiporus* (after Mortensen).

5a–d: Chronological succession in late Paleozoic species of the brachiopod genus *Punctospirifer,* respectively *P. kentuckiensis* (early), late form of same, *P. angulata,* and *P. pulcher* (diagrammatic).

6a–8b: Chronologic succession in Paleozoic lineage of rugose corals, respectively, primitive *Zaphrentis* sp., *Caninia* sp. and *Siphonophrentis* sp. (diagrammatic).

then it is evident that much greater emphasis than formerly may profitably be placed on size changes in these forms.

Corals

Although little attention has been given to the significance of size in the skeletons of corals, it is clear that gradual increase in dimensions is a common trend in the coralla of solitary forms and possibly (but less certainly) also in the gross dimensions of the compound skeleton of colonial forms. This trend appears to be most conspicuous at the level of genera, where absolute dimensions are more or less characteristic of species. This is particularly true in the Paleozoic Rugosa (e.g., *Streptelasma, Zaphrentis, Caninia, Lophophyllidium,* etc.), but also is well shown in the history of the Scleractinia (stony hexacorals) which show size increase in many stocks of solitary forms since the first appearance of their relatively small ancestors in the early Mesozoic. Examples are found in the genera *Oppelismilia, Leptophyllia, Cyclolites, Fungia, Stephanophyllia, Montlivaltia, Trochosmilia, Flabellum,* and *Axosmilia* (*fide* John W. Wells, personal communication).

There are other evolutionary tendencies among the solitary tetracorals, which are commonly associated with progressive increase in size. Some of these may be allomorphic. These trends include:

(1) Change from marked bilateral symmetry, so characteristic of primitive tetracorals, to radial symmetry
(2) Increase in number of septa
(3) Progressive shortening of the septa so that they no longer reach the central part of the calyx (amplexoid trend)
(4) Development of abundant marginal vesicular structures (dissepiments)
(5) Development of axial structures
(6) Change from turbinate to subcylindrical form

Until adequate quantitative studies have been made it is not possible to state to what extent these and other evolutionary trends in the tetracorals are a result of gradual increase in size. Inspection of the record, however, shows that there is at least imperfect correlation in many instances; hence, these trends must be to a degree dependent on size increase.

A common evolutionary trend in Paleozoic solitary Rugosa (tetracorals) is a gradual change from turbinate or trochoid, to cylindroid form of corallum (Lang, 1923). This is so generally related to increase in size that the view is very common among students of these fossils that all cylindroid forms were developed from smaller trochoid ancestors. A correlation between form and size is well shown in the phyletic series of certain genera of the family Zaphrentidae, *Zaphrentis-Caninia-Siphonophrentis* (fig. 1, 6a–8b). Corallites of species of *Zaphrentis* (Silurian-Mississippian) are trochoid, and primitive representatives commonly measure less than 15 mm. high, although advanced forms several times these linear dimensions are known. Corallites referred to *Caninia* (Devonian-Pennsylvanian) typically are cylindroid, although some investigators include also certain trochoid forms within the genus. Characteristic representatives rarely are less than 20 mm. in diameter and 100 mm. high at maturity. Size increase reaches a maximum in cylindroid corallites of *Siphonophrentis* (Devonian) and the related *Siphonophyllia* (Devonian-Mississippian), which reach an extreme diameter of the order of 60 mm. and a height of 750 mm. Although adequate quantitative data on corallite dimensions are not now available, it is clear that there has been pronounced increase in mean size in this lineage of Zaphrentids.

At a lower taxonomic level similar trends are found within single genera, for example: *Streptelasma corniculum* Hall, a mid-Ordovician turbinate species, is replaced in the late Ordovician by much larger cylindroid corallites of *S. rusticum* Billings. And the trochoid coral *Lophophyllidium wewokanum* Jeffords of middle Pennsylvanian age is replaced in the late

Pennsylvanian by a larger cylindroid *L. plummeri* Jeffords (Jeffords, 1947).

Bryozoa

The individual animals of bryozoan colonies show surprisingly limited range in size. From the earliest appearance of fossil representatives of these animals some four hundred million years ago (late Cambrian) they have been distinguished by conservatism and standardization in many features, and they also are characterized in general by very low rates of evolution. Some forms apparently remained well adapted during immense spans of time. Nevertheless, there are well-defined examples of slight but persistent size increase in the extinct order Cryptostomata, the group which includes the lacy fenestrate forms of the Paleozoic.

We are indebted to M. K. Elias (1937) for a well-documented and convincing demonstration of this trend in Pennsylvanian and Permian species of the genera *Fenestrellina* and *Polypora.* In both groups compact lineages show a limited tendency for uniform size increase of most of the zoarial elements. Elias notes that an exception is found in the dissepiments, which do not increase in width (*op. cit.*, p. 312). Apparently these structures show negative allomorphosis.

Evolution in *Fenestrellina mimica, Polypora elliptica,* and their near relatives, consists essentially in stretching of the zoarium in all directions within its plane, as a result of which, distances between branches, dissepiments, zooecia, and nodes gradually increase with advancing geologic time (Elias, *op. cit.*, p. 312). This increase is not, however, "as if the typical—zoarium of these—species were uniformly magnified with the advance of geologic age" (*op. cit.*, p. 312) since the absolute rates of change are greater in some characters than in others. The interrelations appear to be allometric, and it is probable that changes in proportion are the consequences of the factors which cause gradual increase in size (fig. 1, 3a–g). Although Elias did not record mean

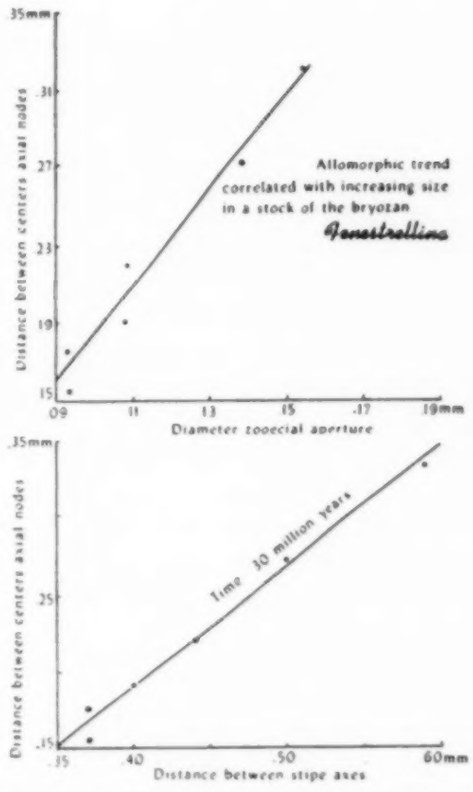

FIG. 2. Allomorphosis in species of late Paleozoic bryozoan *Fenestrellina* (data from Elias, 1937).

values for the diameters of the zooecial apertures his diagrams show that they also progressively increase in size (fig. 2). The apertures undoubtedly are proportional in size to the dimensions of the individual animals of the colony. Probably the size increase and concomitant changes in zoarial proportions in these lineages are consequential on selection for increasing size in the parent individual or sexual generation (ancestrula) of the colony. The rate at which the recorded trend evolved from earliest late Pennsylvanian to early middle Permian was about 100% increase in a total of 20 to 30 million years.

Brachiopods

Brachiopods have not often produced giants during their history, yet the largest forms (*Gigantella,* 300 mm. ± wide) are more than 300 times the linear dimensions of the smallest. Increase in size on a modest scale is a prevalent trend among articulate brachiopods on specific and gen-

eric levels, and less commonly at the level of families. In a few examples that come to mind it appears highly probable that some trends in evolution are really secondarily dependent upon increasing size. But quantitative data are lacking to test this theory. By the nature of the case neither maximum nor mean dimensions are generally available in fossil brachiopods, nor for that matter in most other groups. Therefore, the following comments must be regarded as a subjective appraisal.

Some stocks of the Terebratuloidea developed individuals of relatively large size early in the history of the order, during the great eruptive phase in the Devonian. These culminated in robust shells belonging to *Amphigenia, Rensselaeria, Stringocephalus* and related forms. The largest shells of species referred to these genera exceed in linear dimensions their late Silurian and early Devonian ancestors in the order of about five times in some 40 million years.

A similar trend in the Pentameroidea culminating in *Pentamerus* and *Conchidium* is seen in the early and middle Silurian, when linear dimensions increased about three times during approximately 20 million years. The Mississippian Productacea produced some of the largest brachiopods known. Starting with the small late Devonian and early Mississippian *Productella* some 20 mm. in width, this development toward large individuals reached a peak near the middle of the period in shells of the genus *Gigantella,* about 300 mm. across. This is an increase of linear dimensions about fifteen times in 20 million years. During the late Paleozoic a number of genera of Productids independently produced forms 70 or 80 mm. across.

An interesting development within the Productacea is the aberrant family Richthofeniidae which originated in early or middle Pennsylvanian time from a small Productid (*Marginifera*) probably less than 15 mm. wide, with convexity (or depth) of 10 mm. In the derived genus *Teguliferina* the ventral valve is in some species larger and it became deeper and subconical, and the dorsal valve became modified into an operculum. The Permian forms belonging to *Prorichthofenia* and *Richthofenia* are so highly modified that they closely resemble solitary corals rather than brachiopods. In these forms the ventral valve is elongate-conical to subcylindrical and at the margin it extends well beyond the operculum, forming a capacious vestibule betweeen the aperture and the dorsal valve. The depth of the ventral valve may be taken as a measure of size because it is this dimension which greatly increases during evolution. If 10 mm. be taken as the convexity of the ventral valve in the ancestral *Marginifera,* and 50 mm. the convexity or depth of a ventral valve in a large *Richthofenia,* then the increase in this dimension has been about five-fold during some 40 million years.

Probably the commonest expression of size increase in the evolution of brachiopods is at a low taxonomic level where representatives of a species show a tendency for increasing robustness at progressively higher stratigraphic levels. Distinctive populations have been given trinomial names or, where there are large gaps in the record, they have been designated as separate species. Phyletic growth at this level is illustrated by *Rafinesquina* in the middle and late Ordovician forming the series *R. trentonensis, R. nasuta, R. ponderosa, R. loxorhytis.* The increase in hinge length is roughly 2½ times in 30 million years. Shells of species of *Platystrophia* and other genera similarly increase in size during the same span of time, that is, middle and late Ordovician. "The varieties" of *Pentamerus laevis* in the middle Silurian, *Chonetes* spp., and *Punctospirifer* spp. (fig. 1, 5a–d), show progressive size increase in the Pennsylvanian and Permian rocks. Species of the latter genus show a five-fold increase in width during the 30 million years from middle Pennsylvanian to middle Permian time.

The trend for increasing size during the

late Paleozoic is well shown by a large number of brachiopod genera. Most of these begin in the early Pennsylvanian or late Mississippian and show progressive increase in linear dimensions throughout the Pennsylvanian and Permian.

At present we can only speculate regarding the degree of correlation between size increase and other trends, such as changes in form, ornamentation, structure of cardinalia, and form of brachial structures, because no attempt has been made to determine the extent to which these trends are inter-related. Rensch (1948) has shown that phyletic increase or decrease in size commonly has important subsidiary effects. These subsidiary effects, however, may show only imperfect correlation with size since these characters may be separately determined by natural selection, and selection pressure may fluctuate with changes in size.

Further examination of the record of brachiopod evolution by specialists is needed in order to evaluate the importance of allomorphic trends correlated with phyletic increase in size.

Echinoderms

Phyletic increase in size has been an important trend in the evolution of the echinoderms. In a general way it is clear that large living starfish (up to 350 mm. ± between tips of fully extended rays) are about five or six times the size of large Paleozoic forms (e.g., *Devonaster*), and Mesozoic starfish are of intermediate dimensions. The oldest known representatives of the Stelleroidea are small Ordovician forms about 15 mm. in diameter (e.g., *Hudsonaster*). The main changes which took place among these earliest forms were increase in size accompanied by an extension of the central disk (effected by incorporation of the proximal portions of the arms), elongation and broadening of the arms by increase in the size and number of plates, and a general disproportionate increase of the internal capacity of the body. These changes were accompanied by a multiplication of ambulacral plates, implying an increase in the number of podia with resulting increase in ambulatory and respiratory efficiency.

Later, in the Cretaceous period, there was a general tendency in unrelated stocks toward increasing the internal capacity of the body by increasing its depth. Many of these changes appear to be concomitant with increasing size. The extent and degree of correlation between size increase and other modifications has not yet been determined, but the circumstantial evidence indicates that correlation may be high.

The Echinoidea show limited tendencies for increase in size during evolution. The largest known echinoid is a living form about 200 mm. in diameter (*Echinus esculentus,* fide Mortensen, 1943). It is also true that the largest known representatives of many, but by no means all extant families, are living forms.

Cidaroidea of Triassic age were pygmies according to Mortensen (1928), but this order very soon developed giants during Jurassic time (*Rhabdocidaris, Diplocidaris*). Some of the Holectypina (*Pileus, Holectypus giganteus*) which certainly developed from small Triassic ancestors, produced giants during the Jurassic measuring 150 mm. and more in diameter (Mortensen, 1948).

A particularly well-documented illustration of phyletic increase in size is shown by the remarkable order Melonechinoida, which appears to be limited to part of the Mississippian period. These are symmetrical, globular echinoids which show rapid evolution through a succession of five genera (*Palaeechinus, Maccoya, Lovenechinus, Oligoporus, Melonechinus*), distributed at successive horizons in the early and middle Mississippian of North America and Europe, and representing a span of time of about 20 million years. Morphological specialization corresponds closely with the geological succession. Evolution in the Melonechinoida includes progressive increase in size from a transverse diameter of about 45 mm. in

species of the most primitive genus *Palaeechinus* (fig. 1, 4a) to 155 mm. in the culminating genus *Melonechinus* (fig. 1, 4b). Intermediate genera are represented by individuals of intermediate dimensions. Attendant effects include changes in form and increase in the number of radial columns of plates that compose the corona. The number of columns of ambulacral plates which bore the tube feet increased in number from ten, in primitive forms, to about forty in advanced species, possibly resulting in overall increased biological efficiency, but it is clear that a large form must have more tube feet than a small one to function equally well. Some of these modifications may approximate allometric patterns.

Progressive increase in size during evolution is a not uncommon trend in crinoids. According to Moore and Laudon (1943, p. 20) "noteworthy, but less definite than other evolutionary changes, is an increase in the average size of specimens and, later on, a decrease. The geologic age of the most robust representatives of any large group of Paleozoic crinoids coincides approximately with the time of maximum differentiation and profusion of the group." It has not yet been determined, but it seems possible, if not probable, that the increase in complexity and number of elements incorporated in the crinoid skeleton may be closely correlated with increase in body size during phylogeny. Further support for this theory seems to be found in the fact that many lineages of crinoids undergo secondary simplification in the arrangement of plates in the calyx after the maximum differentiation has once been attained. In some of these forms there is a concomitant decrease in size.

In a scholarly treatise on the Permian crinoid *Calceolispongia* Teichert (1949) has described a striking tendency in this genus for development of progressively larger forms with passage of time. Through about 7000 feet of middle Permian (Artinskian) strata in Western Australia, thirteen species were discriminated, each characterized by an increase in robustness over stratigraphically lower forms. During an estimated six million years the basal plate of the calyx shows increase in volume of 40,000 per cent (fig. 3). According to Teichert the basal plate increased in bulk at a rate greater than the calyx as a whole, but because of the imperfect preservation the data on calyx dimensions are not sufficient for analysis of the allomorphic relationships.

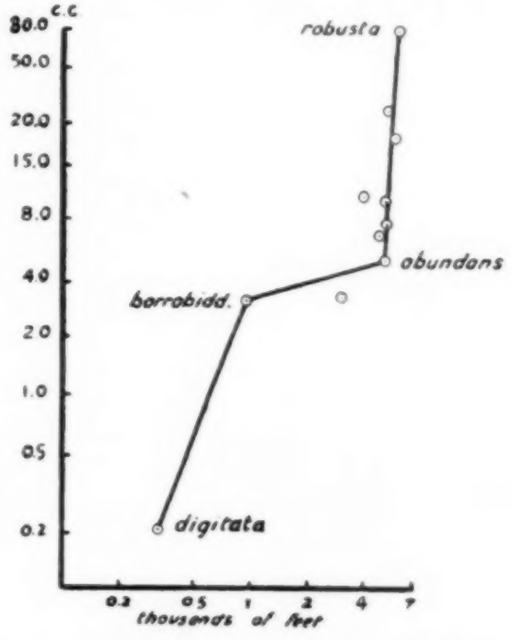

FIG. 3. Phyletic growth in the Permian crinoid *Calceolispongia* (Teichert, 1949). Volume increase of basal plate plotted against thickness of strata.

Mollusca

It is well established that among the molluscs there are countless phyletic lines which have progressively increased the dimensions of the individuals during much or part of their evolutionary history. It appears that the largest cephalopods, the largest gastropods, the largest pelecypods and probably the largest chitons that have ever lived are represented by existing species. This fact, of course, is not nearly so significant as the general tendency for an increase with time of mean size of individuals in these groups. Although quantitative data are not readily available, stu-

dents of Mollusca are impressed by the comparatively small size of older species in a large number of groups as compared with their younger descendants. Paleozoic gastropods and pelecypods are relatively small as compared with those of the later Mesozoic or Tertiary, and, of course, Mesozoic ammonites are conspicuously larger than their Paleozoic ancestors.

Comments on phyletic growth in the molluscs, for the purpose of the present discussion, will be limited to the pelecypods and ammonoid cephalopods, where the record is clearest.

Phyletic increase in size is well shown by many pelecypod lineages. In some cases the trend is more or less characteristic of entire families, mainly in post-Triassic time. It seems that mean size of individuals has gradually increased to a maximum, followed in some cases either by extinction of the whole group or of the larger forms. Such families include, among others, the Ostreidae, Megalodontidae, Unionidae, Trigoniidae, Pectinidae, Spondylidae, and Limidae. In some cases even entire superfamilies such as the Chamacea and Rudistacea, which are typically sessile, reef-dwelling pelecypods of half a dozen or so families, show a very prevalent tendency for size increase during evolution. In almost all of these genera advanced species are represented by individuals that are more robust than the immediate ancestors. Naturally, there are exceptions to this generalization. Phyletic size increase, within genera, is striking in the Jurassic *Diceras,* Tertiary and Recent *Chama,* and the Cretaceous genera *Monopleura, Caprina, Hippurites,* and *Radiolites* and their relatives. In most of these groups the most advanced species are several times the linear dimensions of their ancestors.

In the most advanced order of pelecypods, the Teleodesmacea (or Heterodonta), there are scattered examples of phyletic growth. Most of the families originate in the late Paleozoic and Triassic, such as, for example, the Carditidae, Lucinidae, Corbidae, Cardiidae, Veneridae, and Tellinidae. In practically every

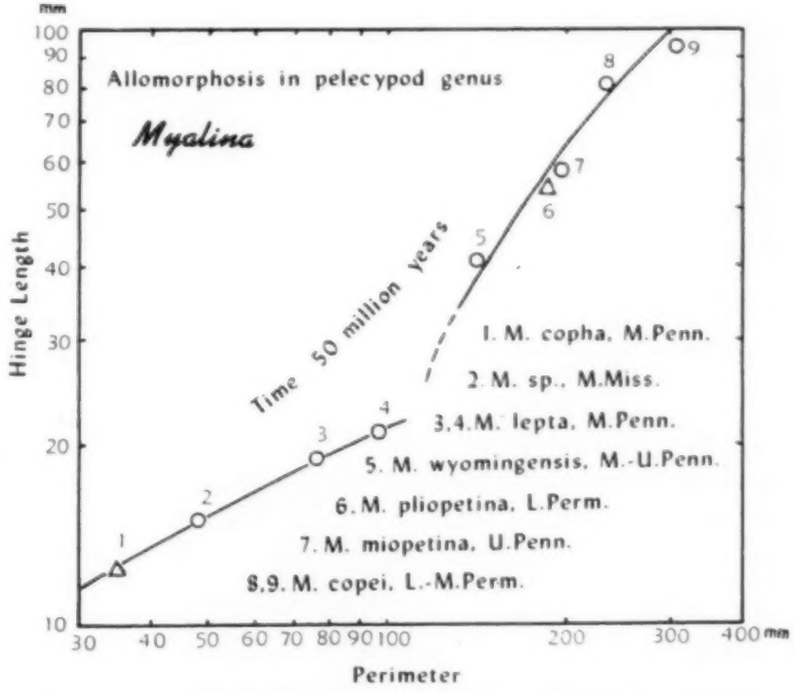

FIG. 4. Allomorphosis in species of late Paleozoic pelecypod *Myalina* (data from Newell, 1942). Size increase corresponds well with chronology, except in numbers 1 and 6, which are exceptionally small for their stratigraphic positions.

case the early representatives are appreciably smaller than the Cretaceous and Tertiary descendants.

Typical features of the pelecypod shell, such as details of ornamentation, and dentition of the hinge, are sometimes regarded as "non-adaptive" structures. Is it not probable that much of the evolution of form, ornamentation, and shell structure in pelecypods is directly or indirectly a result of size increase? Studies on this subject have yet to be begun.

Evolution in late Paleozoic pelecypods of the genus *Myalina* illustrates how shell form may be modified during phyletic increase in size (fig. 4). As shell size increased in these forms, an extension or auricle developed along the rear end of the hinge margin. As so commonly is the case in molluscs, the ontogeny of the geologically youngest form repeats rather closely some of the stages in phylogeny. If the changes in form during phylogeny were allometrically correlated with increasing size, these changes plotted against size should, according to the allometric formula, form the connecting points on a simple regression curve. The fact that the plot is a complex curve or, in fact, two curves (fig. 4) suggests that hinge length was especially favored by selection in the later evolution. At the same time it is perfectly clear that hinge length is correlated with size, and probably the allometric relation is the result of size increase.

Phyletic size increase is well known in many stocks of ammonites. It was long ago established as a rough qualitative statement that a large number of lineages are characterized by a marked tendency for size increase during evolution. Shells reaching a maximum of almost 150 mm. in diameter of the phragmocone, occur in the Devonian, Mississippian (*Agoniatites*), and Pennsylvanian (*Glaphyrites*), but they are rare exceptions, and shells more than 75 mm. in diameter are comparatively uncommon. Permian forms 150 mm. across are common in several families, and shells of 250 mm. or more across the phragmocone are known (*Medlicottia, Cyclolobus*).

From early to late Triassic time a number of stocks rapidly followed the trend of increase in size. In the early Triassic, forms with ceratitic sutures (e.g., *Meekoceras*) commonly attain a diameter of 200 mm. and more through the disk of the phragmocone. These forms clearly were derived from smaller Permian types. Pinacoceratidae exceptionally attained 800 mm. or so in the late Triassic, and it is of interest in this connection to note that a species of *Pinacoceras* possesses the most complex suture pattern of any ammonites. During some 35 million years of the Triassic period the increase of shell diameter was of the order of 400 per cent. Large ammonites are even commoner in the Jurassic than in the Triassic, and some of these (Perisphinictidae) attain dimensions of 500 mm. to 800 mm. in diameter near the close of the Jurassic. It is clear that there was a marked increase in mean size of shells. Gigantic ammonites are well known in the early Cretaceous, but an all-time maximum was reached in the late Cretaceous time at the twilight of ammonite history. Quite a number of species in the late Cretaceous have produced individuals with phragmocones of the order of one meter in diameter. Most of these giants belong in three families of ammonites: Engonoceratidae, Desmoceratidae and Diploceratidae. The largest ammonite shell on record has been referred to *Pachydiscus? seppenradensis* Landois from Westphalia (Miller and Youngquist, 1946). This shell measures about 1800 mm. across the disk of the phragmocone and restored to include the living chamber is estimated at 2550 mm. in diameter.

These figures signify that there has been a progressive increase in maximum size of individuals during the evolution of the Ammonoidea. Much more significant is the fact that a mean size increase during phylogeny is shown by a large number of families, perhaps the majority of phyletic lines recognized within the whole order.

One of the most interesting aspects of ammonoid evolution has been the progressive elaboration of the suture pattern—an expression of plication of septal margins. This has been ascribed to orthogenesis by the older writers, and hence, was regarded as non-adaptive in origin. A commonly stated selectionist view holds that crenulated septa are stronger than unmodified septa; hence, septal elaboration is supposed to be an adaptation for shell strength. It seems more likely to me that elaboration of the septa, reflecting crenulations of the posterior folds of the cephalopod mantle, may to some degree represent progressive modifications for increased efficiency in some physiological function such as, for example, respiration. In molluscs it is rather common for the mantle lining partly or wholly to take over the respiratory function. In fact the gills themselves are nothing more than modifications of the mantle. This theory supplies a logical explanation of the general correlation between suture complexity in a particular lineage and overall shell size because generally it is true that the smaller shells in a given phyletic line have less complex sutures than larger shells.

Since early in the 19th century it has been known that in a broad way basic suture patterns in ammonite lineages increase in complexity from their first geologic appearance until the time of extinction. In many cases suture ontogenies rather closely parallel phylogenies, and this has been adduced as an example of the law of recapitulation (e.g., Miller and Furnish, 1940a). So, in a sense, it is; but the parallelism between ontogenies and phylogenies probably is the result of a fundamental allometry mechanism for suture differentiation correlated with increase of body size during both ontogeny and phylogeny.

Increase of absolute body size in some lineages probably has automatically brought about disproportionate expansion of the surface of the mantle of the posterior end of the body, but this might also be a result of selection. Expansion of the mantle in this region is to a degree accompanied by plication in increasingly complex digitation of the suture pattern. Spath (1930) has shown that some lineages of Mesozoic ammonites exhibit little or no recapitulation. This is not surprising in view of the fact that not all lineages are known to show size increase, and it is readily demonstrable that suture development in some stocks was somewhat independent of size.

I have endeavored to determine the degree of correlation between size and suture complexity in a rather compact stock of late Paleozoic Ammonoidea, belonging to the families Pronoritidae and Medlicottiidae. In figure 5 the length of suture is plotted against shell diameter. The regressions are drawn so that the length of each line is proportional to the diameter of the largest phragmocones reported for the corresponding genus. Theoretically, if suture length were simply a function of diameter of the shell, all of the observed points would fall along a single regression curve. As a matter of fact the regressions of successively younger genera apparently shift to the left. I interpret this to mean that natural selection has established ammonites with progressively decreasing values of b in the allometric relationship. This causes acceleration in development, since a given stage is reached at a smaller size in ontogeny than in phylogeny. On the other hand, it is perfectly clear that suture length is partly a function of shell diameter. In figure 6 the number of suture elements was plotted against shell diameter showing that the sutures are modified not only by progressive increase in size, but also by the introduction of new crenulations during development. Addition of new suture elements appears to approximate allometric constants until maturity is reached. After that stage, which may be at a quarter to one-half of the full size of a large shell, few, if any, new elements are added as the sutures grow progressively larger during later ontogeny. Although it is perfectly clear that in general the larger shells within a given lineage

have the greatest number of suture elements, the correlation is not of a high order. Acceleration of development during phylogeny causes an apparent shift to the left of these regressions as the value of *b* decreases. One result is increase in suture length.

For studies of allomorphosis in ammonites, conch diameter is not a very satisfactory measure of body size, because there is considerable variation in tightness of coiling, or involution, in some groups. Perimeter of cross-section at a given suture stage would be more reliable and would take into account robustness.

Arthropoda

Increasing size as an evolutionary phenomenon is not particularly characteristic of the arthropods. In fact, great groups such as the spiders, insects and scorpions, apparently, have undergone appreciable diminution in size from some of the larger ancestral types. Nevertheless, phyletic growth is impressively shown in at least one of the major divisions, namely, the horseshoe crabs (Merostomata) and their relatives. Comparatively early in geological history the merostomes developed lineages in which it would seem that large size was advantageous in competition against the dominant forms of that time, the trilobites and the cephalopods. Commencing with relatively small forms in the middle Cambrian (e.g., *Beckwithia typa,* some 50 mm. long), and represented by somewhat larger forms in the late Cambrian (*Aglaspis spinifer,* some 150 mm. long), these Cambrian aglaspids (Raasch, 1939) preceded and probably gave rise to the eurypterids which include some of the largest arthropods on record. The earliest true eurypterids are found in rocks of Ordovician age, and these are moderate sized forms, rarely exceeding 200 to 300 mm. in length. In the Silurian and Devonian periods, however, development toward large size was quite rapid and in some genera (*Pterygotus, Stylonurus*) an extraordinary length of nearly 3 meters was reached. These giant eurypterids are not the youngest known, because the group continued with greatly diminished vigor and reduced size into Carboniferous and Permian times. However, it is improbable that any of the later forms were derived directly from the giants, but rather from contemporary parallel less specialized stocks.

Depéret (1907) has called attention to the fact that within the Limulids there also has been rather a consistent tendency for individuals to increase in size during their history: "The interesting little branch of the Limulidae, which takes birth in the Trias with quite small forms, such as the *Limulus priscus* of the Muschelkalk of Bayreuth, continues in the higher Jurassic with types of average size like the *Limulus walchi* of the lithographic stone of Solenhofen, then with the *Limulus decheni* of the Oligocene, and attains the apogee of its dimensions in the *L. polyphaemus,* still existing in the Gulf of Mexico" (Depéret, 1907, p. 203). Depéret's general conclusion seems to be correct. The Devonian *Paleolimulus signatus* (Beecher) has a cephalic width of around 90 mm. in a large specimen (Dunbar, 1923). This is perhaps four or five times as large as the pygmy Triassic forms mentioned by Depéret. Nevertheless, it is quite clear that during the total recorded span of history of the Limulids there has been a net increase in size of perhaps 400 per cent over the linear dimensions of large ancestral forms.

Unfortunately, no attempts have been made to determine the importance of allomorphic effects in the evolution of the merostomes.

The Causes of Phyletic Growth

Body size and selection

It may be safely inferred that various environmental factors are selective for a narrow range of size in all organisms. The results of evolution with respect to size will be, of course, the mean effect of various internal and external factors operating in more than one direction. Un-

der some conditions, small size evidently is advantageous to an animal; under others large size obviously gives the possessor an advantage. But an animal cannot be both large and small, and the resultant must be a compromise of many factors. Indeed, it seems probable that size in some cases may be a by-product of selection for other characters, e.g., delayed sexual maturity, or for rapid growth.

It is not always clear which environmental factors limit extremes of size in a given animal stock. The lower limit in warm-blooded animals presumably is fixed mainly by the energy loss due to radiation which, according to Bergmann's rule, bears an inverse ratio to body size (Bergmann, 1847). From this it follows that a mouse has to consume much more energy than an elephant, relative to its size, to maintain its body temperature. At the lower limits of adult or larval size animals are powerfully acted upon by physical factors of environment that hardly affect larger animals. Surface tension and viscosity of water exert forces greater than the strength of microscopic animals. These small forms are affected directly, and in some cases they are destroyed by exposure to the atmosphere, or by changes in the chemistry and temperature of the surroundings.

Surface reactions are increasingly important as size decreases. This is because of the increase in the area of surface relative to the volume. With reduction in size it is increasingly difficult to maintain a constant internal environment in some measure independent of the external environment. For these reasons minute forms are commonly (but not always) less tolerant to environmental changes than are related larger organisms.

The upper limit of size in terrestrial animals and plants may be determined by gravity, because large forms have to be much stronger relative to their weight than do small forms in any particular environment. Undoubtedly the same factors govern the upper limit of size in amphibious animals which occasionally are fully exposed to the atmosphere and thus are deprived of the buoyant effect of water. This is an illustration of D'Arcy Thompson's principle of similitude: "The 'dimensions' remain the same in our equations of equilibrium, but the relative values alter with the scale" (D'Arcy Thompson, p. 25, 1942).

The factors which limit the maximum dimensions reached by aquatic animals are not so well understood, and probably they vary with different circumstances. Mechanisms peculiar to a given group, such as are employed in circulation, respiration, and feeding, certainly limit size in some invertebrate groups. This is because there are biomechanical limits beyond which a particular system cannot operate efficiently. Ciliary mechanisms necessarily are small, limited by the size of cilia themselves. Marked efficiency of circulatory, digestive, and excretory organs is required, and elaborate skeletal support must be developed in animals of large size.

Many aquatic invertebrates continue to grow throughout life, but in most the rate of growth slackens at a certain stage, which is loosely termed the "adult." Concurrently with changes in growth rate the shape may or may not be somewhat altered. These changes commonly are correlated with the ripening of the reproductive organs. However, a lobster or an oyster may increase its linear dimensions several fold after the attainment of sexual maturity. In such forms size apparently is limited only by the life span of the organism. On the other hand, there are, for example, some protozoans, worms, and arthropods, in which the reproductive act brings an end to adult existence. Directly or indirectly life-span is under the influence of genes, but physiological life-expectancy seldom is realized in nature. We may judge that "unfavorable environment, heterogeneous genetical composition, diseases, enemies, accidents, etc., kill individuals of every population by scores, mostly during the most sensitive stages of development, before they have

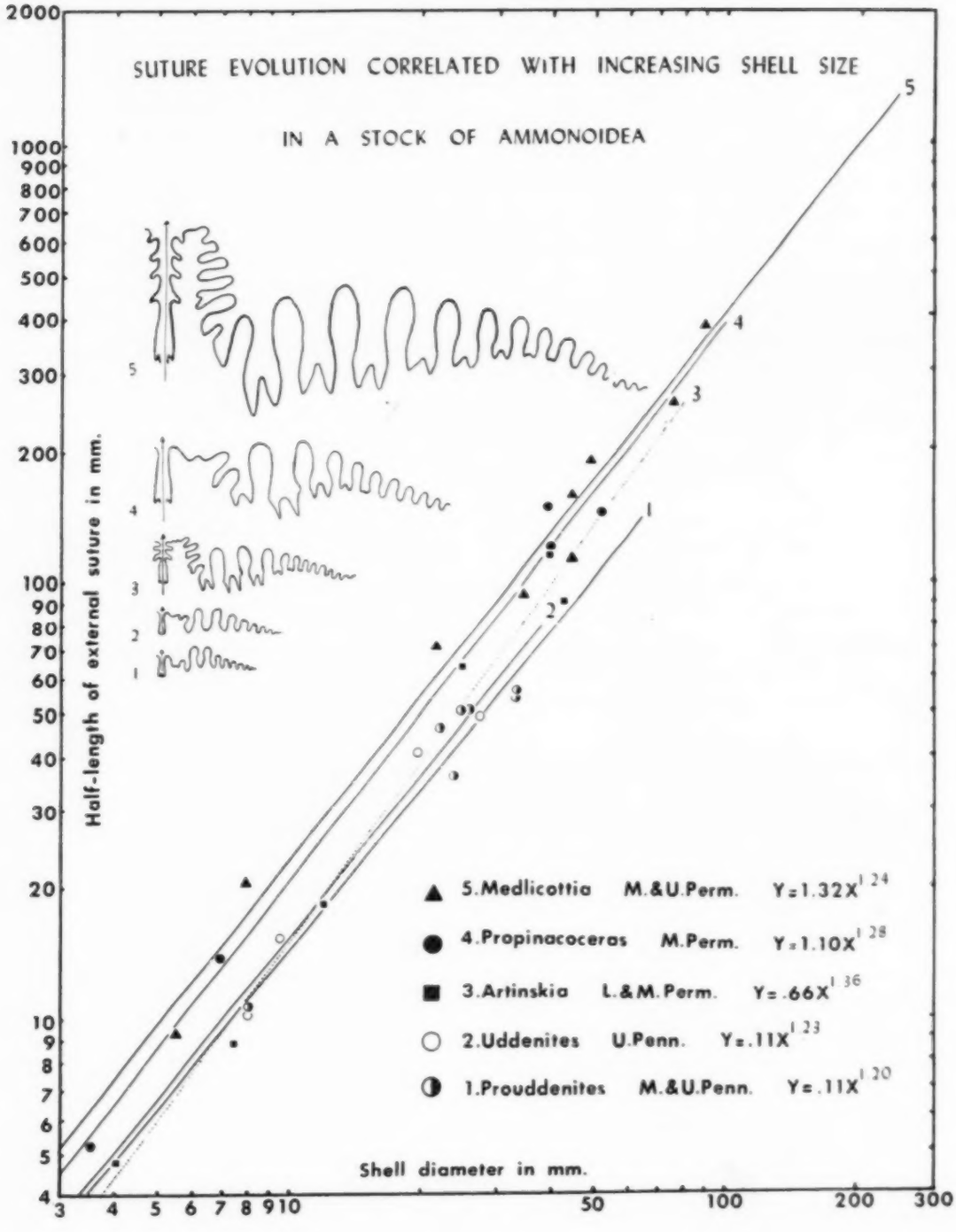
SUTURE EVOLUTION CORRELATED WITH INCREASING SHELL SIZE
IN A STOCK OF AMMONOIDEA
Half-length of external suture in mm.
Shell diameter in mm.
5.Medlicottia M.&U.Perm. Y=1.32X^1.24
4.Propinacoceras M.Perm. Y=1.10X^1.28
3.Artinskia L.&M.Perm. Y=.66X^1.36
2.Uddenites U.Penn. Y=.11X^1.23
1.Prouddenites M.&U.Penn. Y=.11X^1.20

FIG. 5. Allomorphic trend in sutures of late Paleozoic ammonoids.

Data from following sources: *Prouddenites:* Miller, 1930, pl. 38, fig. 6; Miller and Furnish, 1940, fig. 4a; Miller and Furnish, 1940a, figs. 5b–e. *Uddenites:* Miller and Furnish, 1940, figs. 5a–c, 4c. *Artinskia:* Miller and Furnish, 1940, figs. 9a–c, 9f, 8a, 8b. *Propinacoceras:* Miller and Furnish, 1940, figs. 6a–c; Haniel, 1915, figs. 5a, 7a. *Medlicottia:* Miller and Furnish, 1940, figs. 10a, 11b–d, 12b, 13a, 13c, 15a, 15c.

(Note: Perimeter or area of cross section would be better size indices than shell diameter, and should be used in studies of this sort. Unfortunately, conch diameter is the only measure generally available in the literature.)

grown adolescent or mature" (Bodenheimer, 1938, p. 11). Probably mean maximum size in many invertebrate populations is limited by selective elimination of large individuals by predators.

Delayed sexual maturity and phyletic growth

It has been noted that the average rate of growth in the majority of invertebrates is retarded, or in rare cases ceases when sexual maturity is reached. If anything in the internal or external factors tends to delay or to hasten maturation of the gonads without also affecting organism growth-rates, the period of most effective growth will correspondingly be extended or reduced. This directly affects adult size. According to de Beer, "The time at which the adult stage is reached is . . . governed by the rate of action of the genes, either directly, as in the gypsy moth, or indirectly by means of hormones, as in the cases of the frogs and newts. It is possible, therefore, for there to be a competition between the genes which control any particular character and those which determine the assumption of the adult stage, and unless the former work fast enough and get in in time, the character will not be able to show itself. This is what actually happens in those cases in which an animal becomes sexually mature while still in the young stage, a phenomenon known as *neoteny*. . . . On the other hand, by delaying the time at which the adult stage is normally reached, it is possible to cause structures to appear which would not ordinarily have done so" (de Beer, 1940, pp. 20–21).

Growth is greatly affected in many ways by environmental factors, such as salinity, temperature, and food supply, but, of course, the phenotypic modifications directly induced by environment will not contribute to evolutionary trends unless there is selection for a particular variant. Metabolic rates rise with increased temperature, and vice versa. According to Bodenheimer (1938, p. 3), "Speed of development, as well as adult longevity, depends on environmental factors, mainly

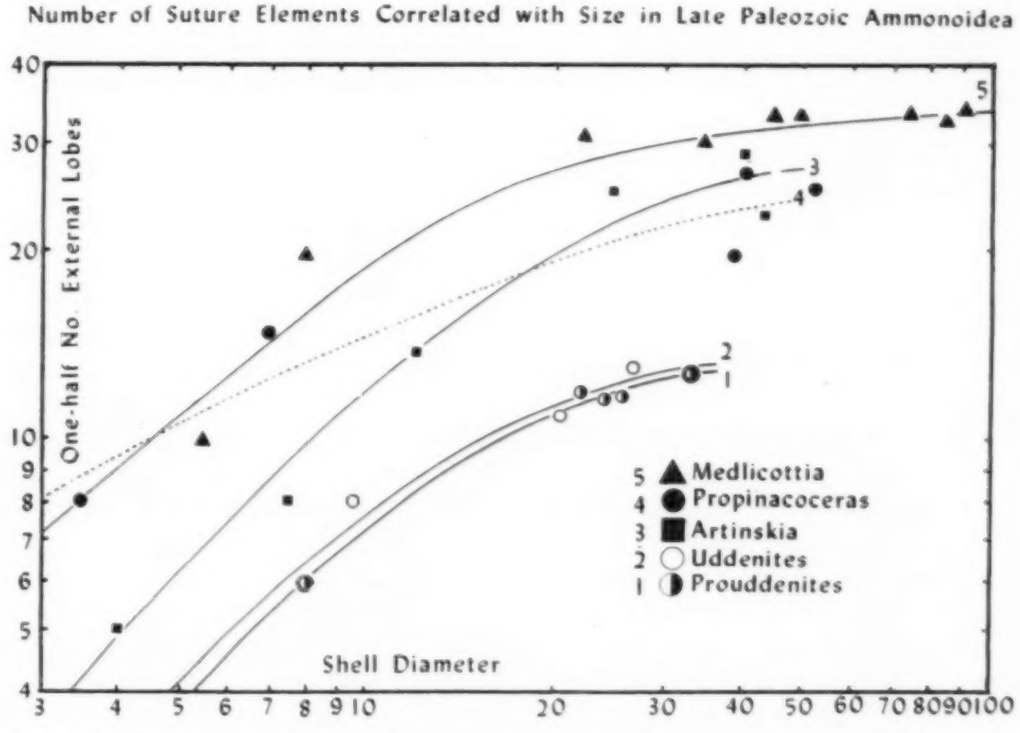

FIG. 6. Total number of lobes (primary, auxiliary, and adventitious on one side of the exterior) correlated with shell diameter in late Paleozoic ammonoids. Sources of data same as in figure 5.

temperature and humidity. High temperatures and optimal humidity shorten lifespan, low temperatures lengthen it."

The rate of gonad maturation relative to body growth appears to decrease with lowered temperatures. Apparently, it is at least partly for this reason that some cold water animals are larger than related warm water forms, both as applies to the races of a wide-ranging species, and to the cold water species which replace tropical forms within a given genus. Delayed sexual maturity, which favors growth in size, appears to be in some way related to the retarding effect of lower temperatures on development in these organisms (Hesse, Allee, and Schmidt, 1937, p. 159). Probably this is related to the general approximate correlation between size and length of generation in animals.

Mann is impressed by the large dimensions attained by numerous Antarctic invertebrates and he lists among these giants examples of Foraminifera, hydroids, echinoderms, worms, pycnogonids, crustaceans, molluscs, and tunicates (Mann, pp. 306–308, 1948). He believes that retardation of ontogeny due to low temperatures, and available rich supplies of food, are important factors in the development of large individuals. Most of these Antarctic giants are treated as distinct species, and it is usually tacitly assumed that in some way large size frequently is an adaptation to the reduced temperatures of the region.

We must not conclude from the above generalization that cold water species, in general, are large, or that warm water forms are generally small, for the statement applies mainly to genera which have representatives in both cold and warm waters. There are many exclusively tropical genera (e.g., Mollusca) which include the largest known representatives of their class. Indeed, the communities of the coral reef are distinguished by the robustness of many of the animals.

Observations on marine gastropods supply additional evidence that there is a close relation between body size and the stage at which sexual maturity is reached. In a British population of the gastropod species *Peringia ulvare* Rothschild (1936) discovered numerous extraordinarily large individuals which displayed irregular growth and other abnormalities. Dissection revealed that in every example the gonads of these giants were damaged or destroyed by nematode parasites. It was concluded that parasitic interference with the normal development of the gonads permitted growth to continue at the high juvenile rate beyond the usual dimensions for adults. A similar situation in *Purpura lapillis* was predicted by Moore (1936) and confirmed by J. B. Knight (personal communication).

In consideration of the above facts it is probable that selective slowing down of the rate of gene action responsible for gonad development would result in increased body size. Strong and continued selection favoring genetic changes of this kind would result in phyletic growth.

Insulating effect of large size

As many investigators (e.g., Carter, 1940, p. 63) have pointed out, probably the most important general advantage of large over small size in animals is the greater independence from the external environment which larger size allows. Protoplasm characteristically requires uniform maintenance of internal conditions unlike those of the exterior. The surface-volume ratio is less in large bodies than in similar smaller ones; hence, the proportion of living tissues in contact with the external environment is less in larger than in smaller animals. Of course, this is an over-simplification. Adaptations to reduce penetration, buffer environment, et cetera, are of paramount importance. But, other things being equal, the large animal can more efficiently maintain the required equilibrium of the life processes than the small one.

Interspecific competition

Undoubtedly, competition, both inter- and intraspecific is an important element in selection for increasing size. The absolute muscular power and defensive armor of large animals almost invariably is greater than that of small related forms. In most respects these give obvious advantages to larger individuals. If animals are active, increase in strength is translated into greater speed which is advantageous in pursuit and flight, and in the search for favorable surroundings. The wider feeding range possessed by large active forms is of survival value during times of food scarcity by providing comparatively greater assurance that food supplies will be encountered. Moore (1938) found that the radius of the area covered by a species of limpet gastropod in browsing on algae varies with the linear dimensions of the individual. In terms of tissue volume it appears that the larger limpets require relatively less food than do small ones.

In some cases the food supply available is more varied for large than for small forms. For example, a small oyster-drill such as *Urosalpinx* cannot feed on thick-shelled clams, and for this reason it will not even attack them. Their food is restricted to thin-shelled forms, which usually are smaller than thick-shelled ones. On the other hand, a large boring gastropod can feed on small and large clams alike. Likewise, a small starfish cannot prey on large clams because of the greater strength and endurance of the latter. The principle seems to be one of general application, and innumerable examples could be selected from most of the Phyla.

Generally, it is true that skeletal parts of large invertebrates are thicker and stronger than those of related small forms. The rate at which a carapace, or shell, thickens relatively to increase in overall body size is fairly characteristic of each group. Thus, there are small animals with thick shells, and large forms with thin shells. Nevertheless, skeletal parts do become absolutely thicker and stronger with increase in size. In addition to their supporting function skeletal parts serve also as armor. Thick-shelled molluscs are relatively more impregnable to attack than are thin-shelled forms, and in any population the largest individuals have the thickest shells.

Intraspecific competition

The majority of invertebrate animals produce far more embryos than can be supported by areas of optimum environment. Those individuals which are fortunate in encountering favorable conditions may survive until the members of their generation come to fill available space, and available food supplies dwindle relative to the needs of a population of growing individuals. Competition between individuals having similar requirements is especially evident in sedentary or sessile benthos, which tend to be gregarious. Larvae of such animals must find a suitable substratum on which to develop or they perish. Castle (1932) has shown that where space and food are at a premium there is likely to be a selective advantage in rapid larval growth and correlated robust size. "There can, accordingly, be no doubt that large body size is an advantage to the individual when in competition with other individuals in early life. Whether it would remain such in adult life would depend upon numerous environmental agencies. It might turn out under some conditions to be a positive handicap as when hunters kill only animals above a minimal size. . . . A supposed orthogenetic tendency to change the proportions in a certain direction is probably, in reality, only a consequence of increased body size, which, in turn, may be a consequence not of orthogenesis, but of competition within the same species, within embryos with slightly different developmental growth rates" (Castle, 1932). Intraspecific competition for food and particularly for living space among less active benthonic animals appears to be a very promising explanation for phyletic increase in size as seen in such attached

forms as brachiopods, corals and bryozoans. It is interesting in this connection to note that generally the so-called embryonic skeletons of the Foraminifera, Bryozoa and Brachiopoda appear to be relatively larger in those forms that ultimately grow to large size at maturity. This shows that the potentiality for growth to large dimensions is present from the earliest growth stages and is the result of sustained high rates of growth.

Groups not affected by phyletic growth

The majority of invertebrate groups have a characteristic mean body size near which all members tend to cluster. In many (e.g., bryozoans, brachiopods, graptolites) there has been astonishingly little size variation for hundreds of millions of years. Even when the trend for phyletic growth is clearly marked, the rate of morphologic change commonly is low. We can conclude only that individual size at the adult stage is strictly controlled by selection. Large variations within a population evidently are subjected, in various ways, to disadvantages which lead to their selective elimination. Small, weaker individuals are at a disadvantage in competition for living space and food. Large individuals, especially conspicuous by their size, are likely to be eliminated by predators, even before reaching sexual maturity.

Lacking adequate data on the biology of living invertebrates, it hardly seems worth while to speculate on the particular selective mechanisms which tend to fix a status quo of mean size. We may deduce that natural selection tends to establish organisms having mean dimensions suitable for the environment in which they live.

Size is one of the more conspicuous phenotypic expressions of the genotype. Mean size tends to be appreciably modified by certain environmental factors, such as kind and quantity of food, salinity of water, and mean temperature. In spite of these mechanisms which produce variability, probably there are relatively few genera of invertebrates in which the linear dimensions of full grown individuals vary by more than 10 diameters. As another guess, it is improbable that size variation within invertebrate species, at equivalent growth stage, commonly varies more than 2 or 3 diameters. It seems that there is very strong selective pressure for mean size and that appreciable deviation from this mean is suppressed by selection. It is not at all clear what the selective factors are, and probably they vary in different groups.

Progressive mean decrease in size during evolution apparently is not a common trend among those invertebrates best represented in the fossil record. Indeed, it is difficult to demonstrate, by means of the paleontological record, that gradual diminution in the size of individuals is characteristic of any particular group. Nevertheless, this may be partly a defect of paleontological records and methods. Many groups of small organisms highly specialized in most respects (e.g., rotifers, small insects, mites, etc.) are essentially without a fossil record. With any given method of collecting, small fossils are more likely to be overlooked than are large ones; hence, the discovery record is relatively less complete for the former.

Summary

Increase in the mean size of individuals during evolution is a widespread phenomenon, affecting many very different groups throughout the animal kingdom. This trend has been given considerable attention in studies of vertebrate evolution, but it has been generally overlooked or neglected by students of the invertebrates. In spite of this it may well be the most important of all invertebrate trends.

Phyletic size increase is of great interest in studies of evolution because allometric effects (allomorphosis) correlated with increase in size may produce subsidiary trends, some of which may be more impressive, but basically less significant than size increase.

It appears that allomorphic trends need not, and commonly do not, show a constant relation to changes in body size, because mutation and natural selection may result in pronounced changes in the allometric constants of organ systems or individual organs, and the selective effect undoubtedly varies in intensity as an organ evolves.

Recapitulatory effects are not simply a consequence of the inheritance of ancestral ontogenies, since comparatively few organisms display really close parallelism between ontogenies and phylogenies. Recapitulatory effects seem to be greatest in groups which show pronounced tendencies for phyletic growth (e.g., Mollusca). This is believed to be because of the additive phenomenon (hypermorphosis of de Beer) by which evolutionary novelties tend to make their first appearance late in the ontogenies of lineages affected by progressively delayed maturity.

Selection for increasing size probably is the result of the statistical advantage that slightly superior bulk gives the individuals of some, but not all groups of animals, within a wide range of environmental conditions. Orthoselection and allomorphosis appear adequate, in the present state of knowledge, to account for the striking linearity of many evolutionary trends. There is no advantage in appealing to unknown or metaphysical factors such as usually are associated with orthogenesis.

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MAMMALIAN EVOLUTION IN THE QUATERNARY OF SOUTHERN AND EASTERN ASIA

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Paleontological contributions to the subject of evolution mostly refer to what is now customarily called macroevolution. The paleontologist usually has insufficient material from a particular horizon and locality to establish the variation limits of the population from which his sample was taken. Study of infraspecific variation hence is left more or less to geneticists and taxonomists. However, phylogenetic work on recent material alone has the disadvantage that the time factor cannot be used in the establishment of phylogenetic units. Paleontology introduces the time dimension, but the paleontologist is forced by the incompleteness of his material to use characters for discrimination other than those by which neozoologists distinguish between their species and subspecies. Consequently, the taxonomic literature on recent animals is of little help to him, and he has to determine whether species or subspecies of mammals that are readily distinguishable by the characters of their skin and skull can also be separated on the basis of a single tooth or (part of a) bone. This requires conscientious study of the odontology and osteology of recent material, a work which he is not always in a position to do.

The student of the Pleistocene and prehistoric fauna deals with the immediate forerunners of the animals constituting the recent fauna. Great evolutionary changes are not to be expected, and at best the student is able to trace certain trends in the evolution of the dentition or of the skeleton rarely extending beyond the limits of a species.

Previous to his researches on the Pleistocene fauna of Java, which culminated in the discovery of *Pithecanthropus erectus* (Dubois), Eug. Dubois (1891) spent some years in the Padang Highlands in central Sumatra, exploring caves yielding a mass of isolated teeth of mammals, including man. In the absence of extinct species in the Sumatran cave fauna, Dubois referred the cave deposits to the prehistoric portion of the Holocene. In Java he collected truly Pleistocene fossils as well as prehistoric teeth and bones, e.g., from the Wadjak cave and from Goea Djimbe, res. Kediri, E. Java.

As a matter of fact the Dubois collections contain many species that are still living, either on Java or on the neighboring Greater Sunda Islands. A comparison of the Pleistocene and prehistoric material with that of the recent forms reveals a certain amount of differentiation which the various forms have undergone in the course of time. In the following I shall give examples from five families, viz., the Rhinocerotidae, the Tapiridae, the Hystricidae, the Felidae, and the Pongidae.

Recent Evolution in Malaysian Rhinoceroses

Three species of rhinoceroses are still living in Asia, viz., the Indian *Rhinoceros unicornis* L., *Dicerorhinus sumatrensis* (Fischer) from Sumatra and Borneo, and *Rhinoceros sondaïcus* Desmarest from Java and Sumatra. The two latter species occur also on the continent, as far north as Bengal. Recently Deraniyagala (1946) recorded *Rh. sondaïcus* in the fossil state from Ceylon.

In the cave collection from Sumatra both *Rhinoceros sondaïcus* and *Dicerorhinus sumatrensis* were met with (Hooijer, 1946a, pp. 12–46). The former species is less abundantly represented than the latter. Isolated cave teeth of both species prove to be rather large in com-

parison with their recent homologues. It is remarkable that the prehistoric teeth of *Dicerorhinus sumatrensis* compare well in size with those of a large form of that species from Bengal which goes under the name *Dicerorhinus sumatrensis lasiotis* (Sclater). A single humerus of *D. sumatrensis* from prehistoric Sumatra is more than 20 per cent longer than the mean of humeri of the recent Sumatran form.

In the Pleistocene of Java we find two species of rhinoceroses, the more common of which is *Rhinoceros sondaïcus*. The fossil averages larger than the living form except in its humerus and femur which must have lengthened since the Pleistocene. The transformation of the skeleton is of the same kind as that observed in some phyla of titanotheres (Hooijer, 1946b). The Pleistocene *Rhinoceros sondaïcus* is more of a swift-moving type than the recent; it is "mediportal" in proportions like recent *D. sumatrensis*, while the recent form belongs to the "graviportal" type, exemplified by recent *Rh. unicornis*. Hunting for rhinoceroses must have been an even more dangerous occupation in the Pleistocene than it is now.

The finding of the extremely long humerus of *D. sumatrensis* in the prehistoric cave collection of Sumatra would suggest that the latter species evolved in a direction opposite to that in which *Rh. sondaïcus* evolved, and at a still faster rate.

Rhinoceros sondaïcus was transformed from a swift-moving to a slow-moving animal during the Quaternary; this is an established fact. It must be kept in mind, however, that the fossil bones are from various localities and perhaps not even all from the same portion of the Pleistocene. A tripartition of the Pleistocene of Java into the lower Pleistocene Djetis fauna, the middle Pleistocene Trinil fauna, and the upper Pleistocene Ngandong fauna, has been worked out in recent years by von Koenigswald (1935). *Rhinoceros sondaïcus* is known since the lower Pleistocene, and by studying the skeletal remains from each of these stages in sufficient quantities it must be possible to follow step by step the change in the limb proportions, which goes hand in hand with a gradual diminution in size.

The second species of rhinoceroses in the Pleistocene of Java is not, as might be expected, *Dicerorhinus sumatrensis*, known in the subfossil and recent state from the islands of Sumatra and Borneo, but a representative of the Indian *Rhinoceros unicornis*, viz., *Rh. unicornis kendengindicus* Dubois. The differences between the two forms are but slight, consisting in the less hypsodont teeth, more molarized premolars, and comparatively narrower metaloph of the upper molars in the fossil Javan form as compared to the recent continental form (Hooijer, 1946a, pp. 84–107). The molar from the Djetis fauna of Sangiran recorded as "? *Coelodonta*" by von Koenigswald (1934, p. 193), a photograph of which was kindly sent to me by Dr. von Koenigswald in 1946, belongs to *Rh. unicornis kendengindicus*, and I found the latter subspecies also in the Dubois collection from the middle Pleistocene of Trinil (Hooijer, 1946a, pp. 104 and 107). No upper Pleistocene remains of *kendengindicus* have been made known as yet. Since the fossil form differs from the recent in progressive as well as in primitive characters, the former cannot have been ancestral to the latter.

Recent Evolution in Tapirs, Porcupines, Tigers, and Orang-utans

The excess in size of the subfossil teeth over their recent homologues, shown by the species of rhinoceroses referred to above, is still more evident in the tapir, *Tapirus indicus* Desmarest. The teeth from the prehistoric Sumatran caves almost invariably are larger than those of the recent form. I have described the prehistoric tapir as *Tapirus indicus intermedius* (Hooijer, 1947b) since the dimensions of the cave teeth are intermediate between those of the recent Sumatran tapir and those of the Pleistocene *Tapirus*

augustus Matthew and Granger from Wanhsien, province of Szechwan, China. The fossil Chinese form has exactly the dimensions we should expect to find for the ancestor of the recent Sumatran tapir through the large subfossil race of the same island. The Pleistocene tapir, however, has more molarized premolars than have the subfossil and the recent, which removes the former from the ancestral line of the latter. The Pleistocene tapir from Java, however, is indistinguishable in size from the recent one of Sumatra.

The porcupines give a beautiful example of subspecific advance in the time dimension. At present there is a race of *Acanthion brachyurus* (L.) in Sumatra, viz., *A. b. longicaudum* (Marsden), that is larger than the recent Javan subspecies *A. b. javanicum* Cuvier. Fossil porcupine teeth from Java are larger than those of the recent form from Java but fall within the limits of the recent Sumatran race, and the subfossil Sumatran cave teeth again exceed the recent from the same island in size (Hooijer, 1946c). Porcupine teeth which are larger even than the subfossil Sumatran specimens are known from Pleistocene caves in southern China and Burma, but the evidence is too scanty to proclaim with a tolerable degree of certainty the Chinese fossil form as the forerunner of *Acanthion brachyurus* in the same line of descent.

The recent races of the tiger, *Panthera tigris* (L.), form a continuous cline from Bengal over Sumatra and Java to Bali. In the above-mentioned order of localities they diminish in size; the Indian form is the largest, the Bali tiger the smallest. The fossils throw some light on the history of the races. In the Pleistocene of Java, as well as in the prehistoric caves of Sumatra, we find teeth and bones of the same size as those of the recent Indian form (Hooijer, 1947a). On the islands the tiger has diminished in size since the time of its immigration from the continent. The tiger underwent a similar, but less pronounced diminution of size in China, where, though smaller than the Indian, it is still larger than the insular subspecies. The Pleistocene tiger from Wanhsien in China (the locality where the large *Tapirus augustus* is from) is as large as the recent Indian subspecies. The fossil metapodials from Wanhsien, however, are decidedly more massive than those of the recent tiger; a character which the Pleistocene Chinese tiger has in common with the fossil tiger from Siberia described by Tscherski (1892). The tiger metapodials from the Javan Pleistocene are more slender than those of the Pleistocene continental tiger, demonstrating that while diminishing in general size the tiger got more slender metapodials too. In Java the tiger has undergone a greater diminution in size than on the continent, and the former was already more slender-footed than the continental forms during the Pleistocene. Racial differences already must have existed by Pleistocene times.

The last example of infraspecific evolution to be discussed here is that studied by me in the orang-utan, *Pongo pygmaeus* (Hoppius). More than three thousand teeth were collected by Dubois in the prehistoric central Sumatran caves, beyond the present range of the species which is now confined to northern Sumatra (Achin), and Borneo. The comparison of the subfossil with the recent teeth (Hooijer, 1948) shows that since the time of the deposition of the teeth in the Sumatran caves, viz., in the early Holocene, the mean of the teeth of the orang-utan has become sixteen per cent smaller. In addition, it has been possible to trace several trends in the evolution of the dentition, all stamping the prehistoric orang-utan as a more simian form than the recent, still further removed in dental structure from man in the points which differentiate the recent orang-utan dentition from that of recent man. The prehistoric males had bigger canines relative to those of the females than the recent animals. The lateral incisors were less reduced in relative size, and the anterior premolar in the lower jaw was relatively larger too. Also the excess in size of the second molar over the other

molars, a typically simian feature that is also encountered during the early stages of the evolution of the hominid dentition, was much more pronounced in the prehistoric orang-utan than it is now.

The Pleistocene orang-utan from Java is indistinguishable in size from the recent form of Sumatra, while the Pleistocene form from southern China and Indo-China is decidedly larger than the subfossil form from Sumatra. Thus the Pleistocene continental form is again larger than the Javanese.

Summary

From the above data the following general conclusions can be drawn:

1. Since the time of their immigration into the Greater Sunda Islands (in the late Pliocene or in the early Pleistocene) various species have undergone a gradual diminution in size, accompanied in some cases by essential changes in the structure of their limbs or feet.

2. The decrease in size during the Quaternary is more advanced in Java than it is in Sumatra. Prehistoric Sumatran forerunners of the living species may be even larger than those of the Pleistocene of Java. If, e.g., the tapir or the orang-utan could have persisted in Java up to the present, they would have become smaller than the recent Sumatran form. Neozoologists would have described them as subspecifically distinct as was done with the Javanese races of porcupine and tiger.

Thus it is evident that the subspeciation of recent species is a process that can be traced back into the Pleistocene. The recent races are the diminutive descendants of racially distinct populations that already existed in the Pleistocene. The comparatively slight amount of differentiation undergone by each of the subspecies during the Quaternary pushes the time of origin of the species back into the Pliocene. From this epoch, however, no fossils are known that can be definitely identified as belonging to any of the species dealt with above. Whether or not this is due to the incompleteness of the paleontological record is a question beyond the scope of the present discussion.

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PARALLELISMS IN THE EVOLUTION OF THE SATURNIID MOTHS

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Parallelism or convergence in evolution is so well known that any biologist can list examples of organisms which look alike or have certain similar structures but nonetheless are only distantly related. The best known instances of convergence, such as the similarity of body form of whales and fish, or of foreleg structure of mantids (Orthoptera) and Mantispids (Neuroptera), involve adaptations of very dissimilar animals to similar modes of life. The examples of parallelism found in the Saturniidae are of a different sort, involving independent acquisition of similar characters by closely related moths. The Saturniidae is a particularly favorable group for this study because the survival of numerous annectent forms has made possible a rather clear understanding of the phylogeny of the group. Without this knowledge of the phylogeny, parallelisms such as those discussed below would not be recognizable as such. The purpose of this paper, then, is to list similar characteristics which have arisen repeatedly in the course of the evolution of these moths, and to consider the reasons for this repetition.

The present analysis is based upon a detailed morphological study of the genera of the saturnioid moths of the western hemisphere, and a less thorough study of those of the eastern hemisphere. The full results of this investigation will be published elsewhere. Two South American genera, each known from a single species, are omitted from consideration here because insufficient material has been available to me. Their relationships are roughly known, however, and their inclusion in the study would not materially affect the conclusions.

In the western hemisphere there are 93 genera and subgenera. The number of species is doubtful but there appear to be at least 700 and perhaps 1000 or more good species, many of them with numerous recognizable subspecies.

PHYLOGENY AND DISTRIBUTION

On the basis of a comparative morphological study, in which some fifty characters received special analysis, a phylogenetic tree for the Saturnioid moths was devised. It is believed that this tree (fig. 1) indicates the relationships with reasonable accuracy. Since there are no known saturniid fossils of any significance, the constructuion of such a tree is possible only because of the existence of unspecialized or primitive genera or species in which for some reason evolution of the principal characters ceased. Such forms provide the intermediate or annectent links necessary to establish the relationships of other genera. If certain specialized characters are ignored, these primitive living groups closely resemble the putative ancestral forms. Thus the trees used in this paper are actually only schemes of relationships based on living forms, not phylogenies in time. It is impracticable to discuss in detail here the characters used in establishing the phylogeny; in any case, the details are of no concern to evolutionists generally. They will be presented, however, in a larger paper to be published elsewhere.

The closest relatives of the Saturniidae are the small South American families Oxytenidae and Cercophanidae. These moths lack many of the peculiar features of the Saturniidae, to which family belong all of the other groups shown in the phylogenetic tree. The Saturniidae have been

divided into seven subfamilies as can be seen in figure 1.

Although all of these subfamilies contain primitive genera, the Rhescyntinae as a whole is the most primitive as shown by several characters shared with the family Oxytenidae. For example, the proboscis bears numerous carinate papillae in the Oxytenidae. Such papillae are present also in many Rhescyntinae, but are want-

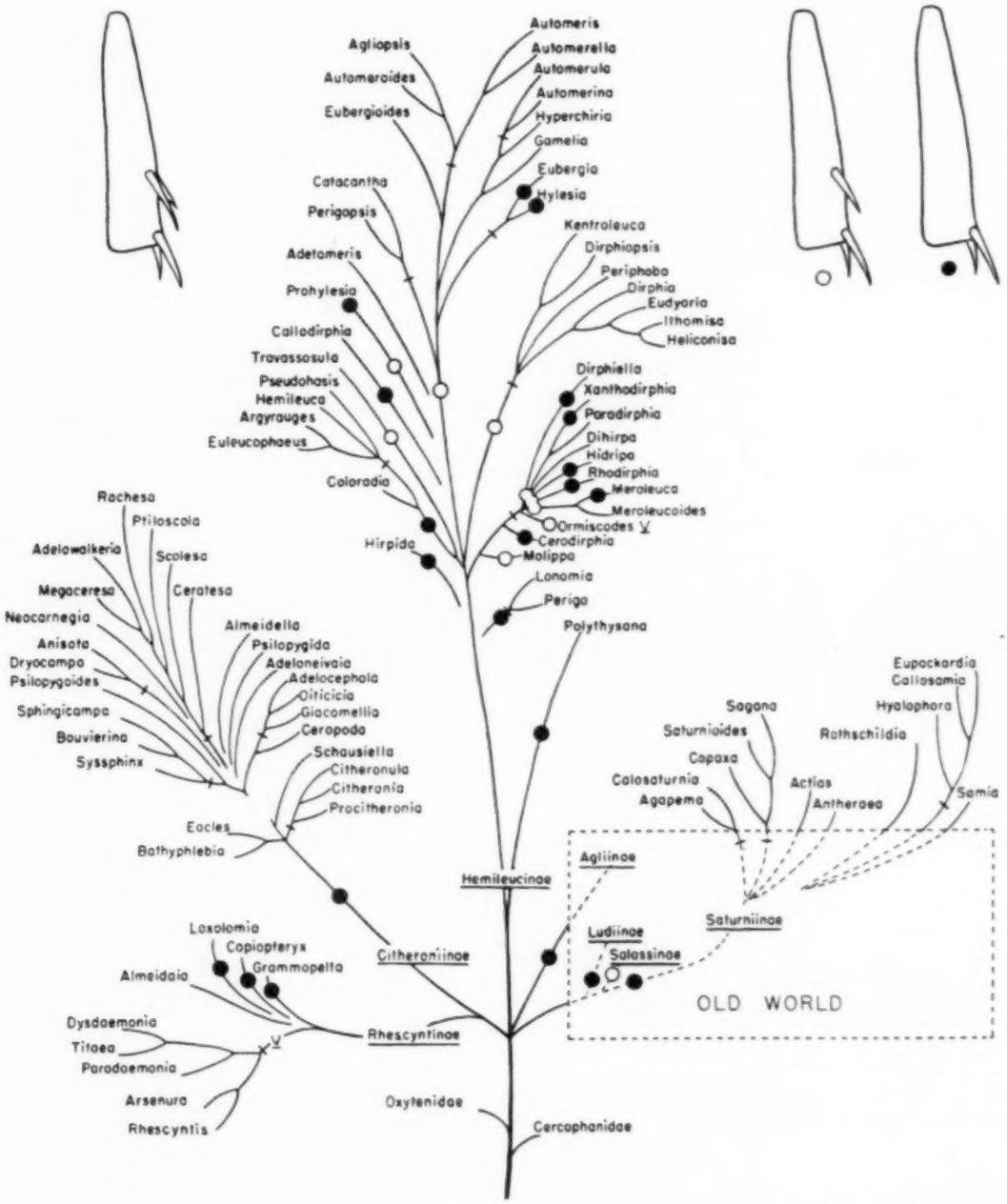

FIG. 1. Phylogenetic tree of the Saturniidae of the New World. The number of subapical hind tibial spurs is primitively two. In forms located beyond a circle there is but one, in forms beyond a black disk there are none. The letter "v" means variable from none to two. Note that *Adetomeris* has two.

A short cross line indicates that the names beyond such a line belong to a single genus and are to be considered as subgenera. Other symbols, if at the end of a line, show that only some species of the genus or subgenus have the character indicated, while if not at the end of a line, they indicate that all forms beyond the symbol have the character.

TABLE 1. *Some of the characteristics of the subfamilies of Saturniidae*

	Rhescyntinae	Citheroniinae	Agliinae	Hemileucinae	Ludiinae	Salassinae	Saturniinae
Frons convex at sides	−	+	−	−	−	−	±
Frontal protuberance present	+	+	−	+	−	+	−
Antennae, if quadripectinate, with apical rami adjacent to basal rami of following segment	+	+	+	+	±	+	−
Antennal cones multiple	±	−	−	−	±	0	+
Pilifers with bristles	+	−	−	−	−	−	−
Anepisternum large	+	+	+	−	+	+	−
Vein M_2 arising in front of middle of apex of cell	−	±	+	+	−	+	+
Larvae with large thoracic horns in early stages	+	+	+	−	−		−
Mature larvae with large thoracic horns	−	+	−	−	−		−

+ Agreeing with statement at left.
− Not agreeing with statement at left.
± Variable, agreeing or not.
0 Structure absent.
In a few cases where a few specialized members of a subfamily have lost a character, this is not indicated in the table.

ing in all other Saturniidae. Numerous other characters indicate the same relationship. The Rhescyntinae are large, broad-winged moths, as are at least the more primitive members of most of the other subfamilies.

It is a relatively minor step from the Rhescyntinae to the primitive members of the Citheroniinae, such as *Bathyphlebia*. The principal characters by which *Bathyphlebia* differs from the more primitive *Rhescyntinae* are the convex lateral margins of the frons, the absence of bristles on the pilifers, the shorter tibial spurs, the absence of the subapical spurs of the posterior tibiae and the absence of tarsal spines. From the large broad winged *Bathyphlebia* the principal direction of evolution in the Citheroniinae has been reduction in size, especially in wing size, so that the more characteristic members of the subfamily are small with the thorax very robust and the wings or at least the forewings slender and powerful so that the shape of the insect as a whole is similar to that of certain Sphingidae.

The remaining subfamilies of the Saturniidae are probably not quite so closely related to the Rhescyntinae as is the Citheroniinae, although in the Agliinae the larval characters are very similar to those of the Rhescyntinae. The adults of the Old World Agliinae, however, are similar to those of the New World Hemileucinae. The subfamily Hemileucinae is the largest of the American groups, and it contains a number of forms (e.g. *Lonomia*) whose relationships are not evident as shown by the broken bases of the lines of the accompanying tree. The relationships of most members of the groups, however, are evident.

The genus *Polythysana* is so different from other Hemileucinae that it has been placed in a tribe by itself and perhaps should be placed in a separate subfamily. While most of its characteristics considered individually can be matched within the rest of the Hemileucinae, the combination of characters is suggestive of certain Saturniinae, except for the wing venation which is not at all like that of the Saturniinae. Probably *Polythysana*, which occurs in Chile, is a relict type, like *Aglia* (Agliinae) and *Salassa* (Salassinae).

The Ludiinae, Salassinae, and Saturni-

inae are rather closely related. In spite of certain specialized characters, most features of the Ludiinae and Salassinae are more primitive than those of the Saturniinae.

Table 1 indicates the more outstanding characteristics of the various subfamilies. It is hoped that, studied in connection with figure 1, this table will give the reader an idea of some of the characteristics regarded as of phylogenetic significance and of the principal lines of evolution in the Saturniidae.

The distributional pattern shown by the various groups of Saturniids is extremely interesting. The Oxytenidae and Cercophanidae are entirely neotropical, all but one genus of the latter family being Chilean. Although the family Saturniidae is almost world-wide except for far northern and far southern regions, its most primitive groups are neotropical. The Rhescyntinae is entirely neotropical. The Citheroniinae is principally neotropical, although a few genera and species extend well north into the Nearctic region. The same is true of the Hemileucinae, although there are more nearctic genera and species than in the Citheroniinae. This great diversity of entirely American groups in the Saturniidae, together with the occurrence in the neotropics of the only families which appear to be very closely related to Saturniidae, suggests that the group as a whole arose in the Western Hemisphere and no doubt in the American tropics.

There are, however, very numerous genera and species of Saturniidae in the Old World, particularly in the Old World tropics. The bulk of these belong to the subfamily Saturniinae which is more richly represented in the Old World than in the New World. The small subfamily Ludiinae, however, is confined to Africa, and the Salassinae to Asia. If one ignores some of the highly specialized features of the Ludiinae such as the reduced size and the reduced labial palpi, the characters of this subfamily might well be regarded as ancestral to those of the Saturniinae. The Salassinae also exhibits primitive characters, such as the frontal protuberance. It therefore seems not unlikely that a common ancestor of the Ludiinae, Salassinae, and Saturniinae reached the Old World not long after the Saturniids became widespread in the New World and that in the Old World it gave rise to the Saturniinae as well as to the modern Ludiinae and the relict Salassinae. The greater part of the evolutionary history of the Saturniinae seems to have taken place in the Old World and, because of lack of material, is not indicated on the accompanying phylogenetic tree. The Saturniinae became wide-spread and eventually, on several different occasions as indicated in figure 1, migrated back into the Western Hemisphere. New World genera of this subfamily are the scattered representatives which were able to migrate from Asia to North America. There are, in fact, three genera of Saturniinae which occur in both hemispheres. All are far better represented in Asia than in America and they may be regarded as having arisen in the Old World and spread to the New World relatively recently. The New World Saturniinae are North American except for *Copaxa* and *Rothschildia* which are well represented in the Neotropics.

The existence of several relict groups has already been indicated. The most outstanding of these are *Polythysana* with four species from Chile (Hemileucinae?), *Aglia* with a single Palearctic species (Agliinae), and *Salassa* with a few species from southern Asia (Salassinae). Each is an exceedingly isolated group. There is a good possibility that *Aglia* and *Polythysana* are related to one another more closely than either is to any other group, in spite of the fact that one is Eurasian, the other Chilean.

The distribution of a group of the more primitive saturniid subfamilies (for example, the Rhescyntinae, Agliinae, Ludiinae, Salassinae, and *Polythysana*) taken together is very discontinuous. The resulting map would be similar to some of

those given by Ander (1942) in his excellent study of the modern distribution of various insect groups represented in the Baltic amber. It seems worth suggesting, therefore, that the saturniids probably arose sometime in the early tertiary or before and may well have been a part of the early tertiary fauna, samples of which are preserved in the Baltic amber.

An interesting feature of distribution of the Saturniidae is their almost complete absence from the West Indies, although the group is extremely well represented around the coasts of the Caribbean and there are a number of species in the southern United States. It is evident that these American forms are poor colonizers of islands. Perhaps this is because the females are relatively sluggish and do not fly much, in spite of their large wings, for there are certainly suitable host plants and climatic conditions in the West Indies. In view of this situation it is interesting that in the Old World the Saturniinae have spread through the East Indies to New Guinea and to Australia.

Reduction or Loss of Structures

Independent variations. The characters discussed below are only a few of the better examples of repeated reduction or loss of structures in the Saturniidae. Many others might easily be cited. In each instance the character has been reduced or lost independently, so far as can be learned, from other characters.

In most moths, including the Oxytenidae, the posterior tibiae bear a pair of subapical spurs in addition to the apical pair. The subapical pair is retained in many members of the large genus *Rhescyntis* (Rhescyntinae) and is retained, or perhaps regained, in *Adetomeris* and some *Ormiscodes,* members of the subfamily Hemileucinae. In all other saturniids, as shown in figure 1, one or both of the subapical spurs are wanting. Both are absent in all members of some of the large groups such as the Citheroniinae and Saturniinae. In the Hemileucinae one is absent in most groups and all stages in the reduction of the remaining one can be found in several genera. As shown in figure 1, the loss of this remaining subapical spur has occurred independently 14 times in the Hemileucinae. Allowing for some misinterpretations of phylogeny, the spur must have been lost at least 10 times.

The epiphyses, or anterior tibial spurs, are frequently lost in the Saturniidae. They are more stable in males than in females, having disappeared in males only four times as shown in figure 2. All groups lacking epiphyses in males also lack them in females. In addition, they are wanting in females of 12 other groups. Assuming the possibility of errors in the phylogenetic tree of the subgenera of *Ormiscodes,* this means that the epiphyses of the female were independently lost at least 10 times during the evolution of the Saturniidae.

The labial palpi in the Saturniidae vary from large three-segmented structures projecting far in front of the head, as in most Lepidoptera, to small one-segmented globules, which may become fused together. The latter condition occurs twice in American Saturniidae, once in *Hemileuca* (Hemileucinae) and once in *Saturnia* (Saturniinae) (shown in figure 3 as *Calosaturnia* and *Agapema,* the American subgenera of *Saturnia*). In the phylogenetic tree (fig. 3) labial palpi are marked as "reduced" in groups in which they extend but little beyond the clypeus and are one- or incompletely two-segmented (feebly three-segmented in *Psilopygoides*). This degree of reduction was reached eleven times according to the phylogenetic tree. If, as seems quite possible, the "Old World" portion of the tree is inaccurate in detail, there nonetheless must have been such reduction in at least eight different groups.

In most groups of Saturniidae the male genital harpes are freely articulated to the ninth abdominal sternum. In the Hemileucinae, however, there is a tendency for the harpes to lose the articulation and become fused to this sternum; they may be

partially fused as in *Automeris* and its allies or completely fused as in *Dirphia* and *Hemileuca*. Some degree of fusion has arisen independently in seven different groups of the Hemileucinae, as shown in figure 3.

The occurrence of parallel evolution in genital structures is noteworthy since they are hidden from the outside and hence presumably relatively little affected by direct selection from the outside environment.

Correlated variations. The characters discussed below involve structures whose reduction or loss is correlated with changes in other structures.

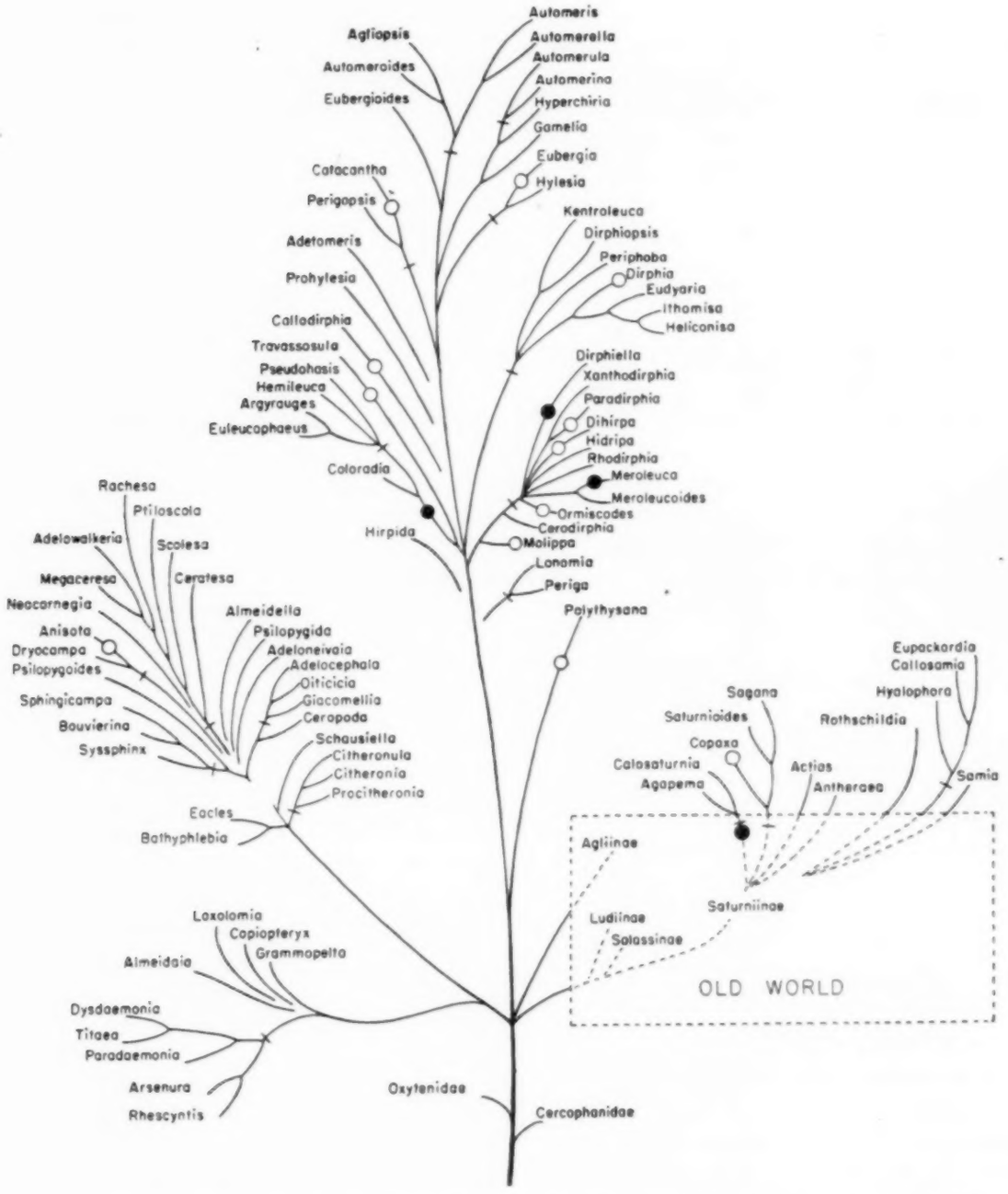

FIG. 2. Phylogenetic tree of the Saturniidae of the New World. Epiphyses are primitively present in both sexes. They are absent in the female in groups marked with a circle, and are absent in both sexes in groups marked with a black disk. For additional explanation see figure 1.

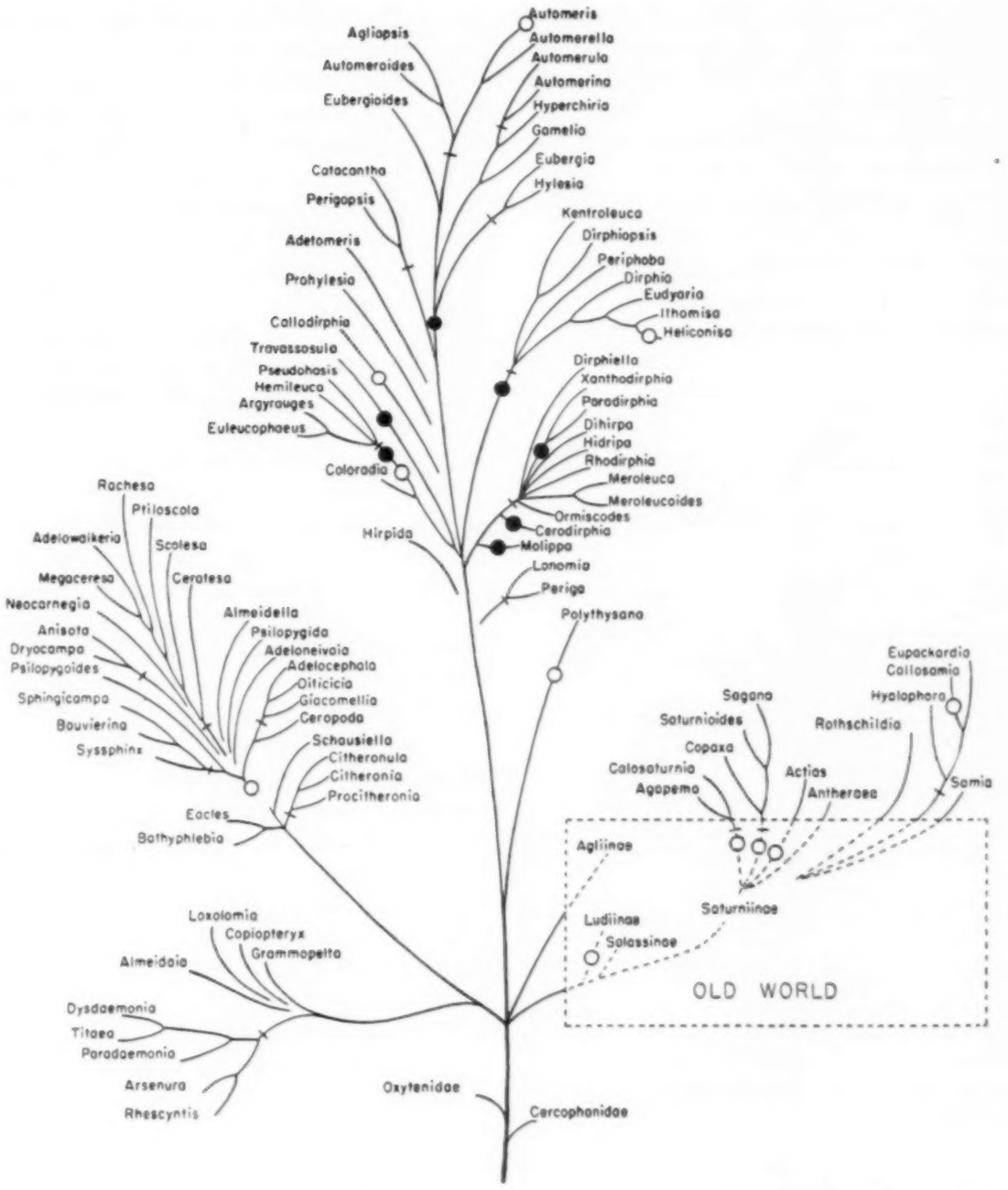

FIG. 3. Phylogenetic tree of the Saturniidae of the New World. The labial palpi are primitively long. They are reduced in forms marked with a circle. The male genital harpes are primitively freely articulated to the ninth segment. They are fused to it in forms marked with a black disk. For additional explanation see figure 1.

In the more primitive Saturniidae the antennae of the male are quadripectinate; that is, each segment bears four projecting processes or rami, a basal pair and an apical pair. In the Hemileucinae there are a number of groups in which the apical rami are reduced or lost. In some groups, especially in certain subgenera of *Dirphia*, every stage in reduction can be observed in different species. The apical rami are lost, that is, the antennae become bipectinate, eight times independently in the Hemileucinae, as shown in figure 4.

Curiously enough, the reduction in the apical rami is correlated with certain characteristics of the basal rami. In forms

with quadripectinate antennae the rami are relatively short and straight (fig. 5) and the setae of the distal rami are directed basad while those of the basal rami are directed distad. When the antennae are bipectinate, however, the rami (basal) are long and strongly curved downward (fig. 5) and their setae are directed downward. When the distal rami are represented by short stubs, an intermediate condition also prevails as to the length and curvature of the basal rami and the direction taken by their setae.

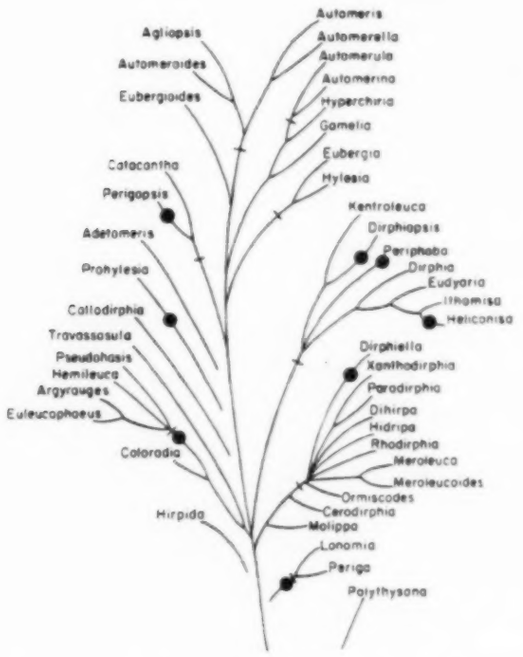

FIG. 4. Phylogenetic tree of the Hemileucinae. The antennae of the male are primitively quadripectinate. In forms marked with a disk they are bipectinate. For additional explanation see figure 1.

FIG. 5. Above: Apical view of an isolated segment of the male antenna of *Automeris*, a form with quadripectinate antennae. Below: Apical view of isolated segment of male antenna of *Hemileuca*, a form with bipectinate antennae.

The eyes of saturniids are large in relation to the head, but their size is variable. As a measure of the eye size, the relation between the length of an eye and the length of the shortest line that can be drawn between the eyes has been used. If the distance between the eyes is one-fifth of the length of an eye, as in some of the Citheroniinae, the eyes are considered very large, while if it is one and one-half times the length of an eye, the eyes are very small. In preparing figure 6 the eyes were considered small if the distance between them were one half the length of an eye or more. It will be seen that this degree of reduction in eye size was achieved 18 times according to figure 6. Even if several of these apparent reductions result from phylogenetic misinterpretations, such reduction must have occurred at least 14 times.

Small eye size is usually correlated with changes in other structures of the head capsule. For example, the ordinarily very small distance between the laterofrontal sutures and the eyes is greatly increased as the eyes are reduced. Moreover, the proboscidial fossa and the frontal protuberance are reduced in all forms with small eyes and in but few others. It is as if the entire head capsule were less fully developed than in ordinary saturniids. Perhaps this is the effect of a group of genes which governs the rate of growth of the head.

Correlated characters of this sort may be very deceptive to the systematist who ordinarily works on the principle that organisms differing by several characters are less closely related than those differing in but one discernible character. It is obvious, however, that the head characters (likewise the antennal characters) described above should be given the weight of but one character even though several differences are involved, for these differences are consistently correlated and behave as a single character.

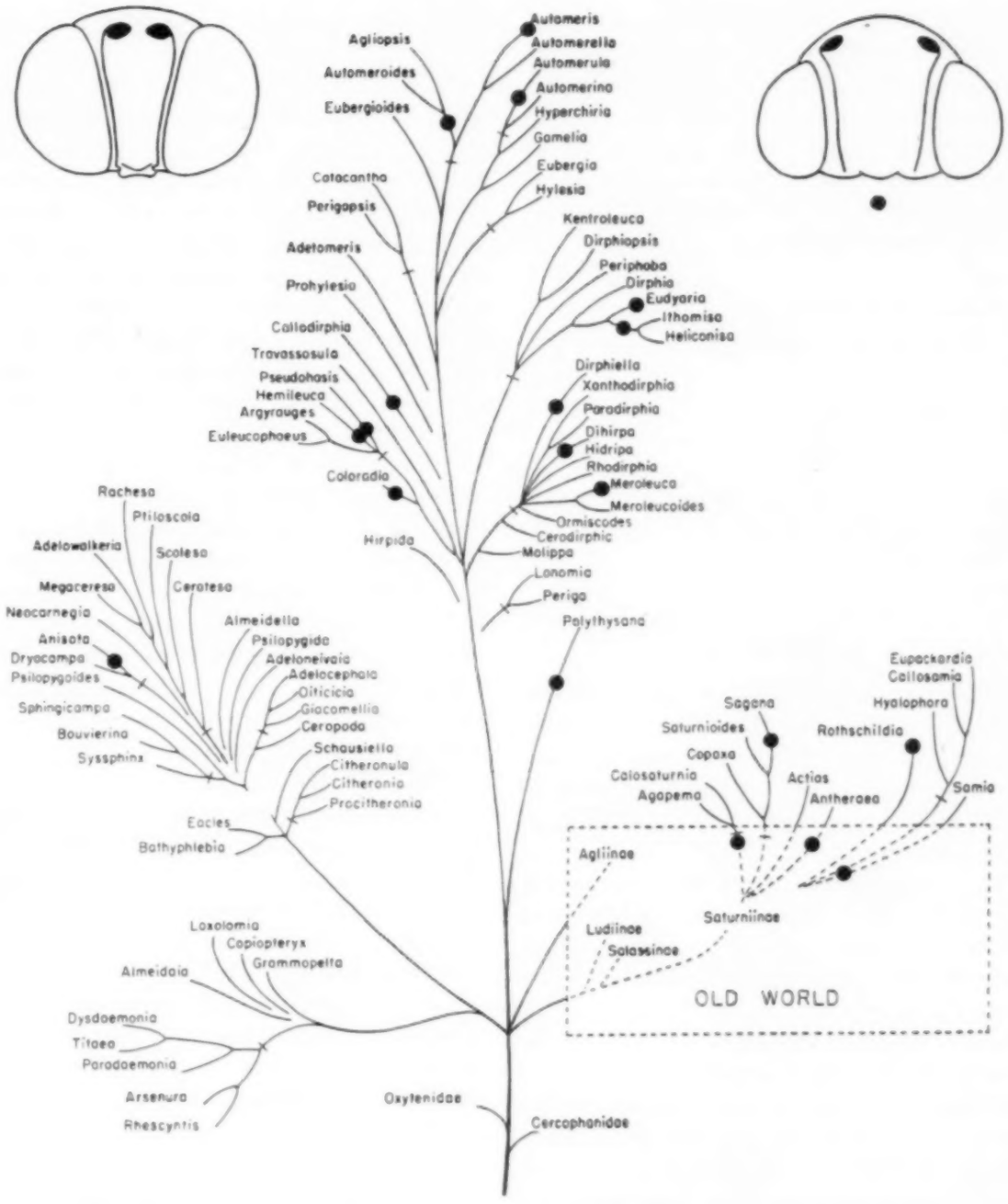

FIG. 6. Phylogenetic tree of the Saturniidae of the New World. The eyes are primitively large. In forms marked with a black disk the eyes are reduced so that the distance between them is one-half the length of an eye or more. For additional explanation see figure 1.

INDEPENDENT ACQUISITION OF A STRUCTURE

The examples of parallel evolution in the Saturniidae described above all involve reduction or loss of certain structures. However, the following example involves the acquisition of a structure found neither in the Oxytenidae and Cercophanidae nor in the more primitive Saturniidae, such as the Rhescyntinae. In these groups the front tibiae are approximately as long as the tarsi and are unarmed (fig. 7). However, as shown in figure 8, there are scattered groups, nine in all, in the Citheroniinae and Hemileucinae in which each front tibia bears a horny spine arising from its outer apical angle (fig. 7).

Some of these groups also have a spine arising from the inner apical angle and even from the apex of the middle tibia. In every case, tibiae bearing such spines are markedly shorter than unarmed tibiae and shorter than the tarsi. Similarly short spined tibiae are found in some Old World Saturniinae.

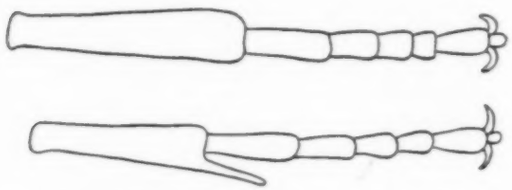

FIG. 7. Above: Normal fore tibia and tarsus. Below: Fore tibia and tarsus of a form with anterior tibial spine.

RELATIVE FREQUENCY OF LOSS AND GAIN OF STRUCTURES

Although the preceding parts of this paper give examples of the loss and gain of structures, they do not give any numerical information on the frequency of loss of old structures or of acquisition of new ones.

In a tabulation of 46 evolutionary trends (table 2), each of which can be observed in one or more parts of the phylogenetic tree of the Saturniidae, it can be noted that there are nearly 3.5 times as many trends toward reduction as toward increase in size of a structure and nearly 10 times as many trends toward reduction as acquisitions of new structures. Many of these trends occur as parallelisms in different groups of the Saturniids, but each is counted but once for the upper row of figures in table 2.

The lower row of figures in table 2 indicates the number of times that such trends have occurred in the Saturniidae of the Western Hemisphere. The differences between the lower numbers and the upper are an indication of the frequency of parallelisms. From the lower figures, it will be seen that trends toward reduction occurred over 5.4 times as frequently as trends toward increase in size of a structure. Trends toward reduction occurred over 8.2 times as frequently as acquisition of new structures. The figure 147, for the number of times which trends toward reduction or loss have occurred, might have been considerably larger. This is because some judgment is involved in determining when a structure is "reduced." For example, labial palpi range from rather long, 3-segmented structures to minute unsegmented spherical bodies hidden under the vestiture. For purposes of this count they were considered reduced when they were 2-segmented but there are some forms with short 3-segmented palpi which might well have been called reduced.

Several examples of reduction or loss of structures have already been given. An example of the increase in size of a pre-existing structure may be seen in the changes in the frontal protuberance. In primitive groups this structure is present as a conspicuous transverse ridge. In scattered groups it becomes a strong snout, a trend recorded in the second column of table 2. Incidentally in other groups it may be reduced or absent (e.g. subfamily Saturniinae) so that the same structure is involved in a trend counted in the first column of table 2.

Under acquisition of new structures are included the tibial spines mentioned in the preceding section of this paper. These

TABLE 2. *Frequency of forty-six different evolutionary trends in the Saturniidae*

	Reduction or loss of a structure	Increase in size of a pre-existing structure	Acquisition of new structure	Not classifiable
Number of trends	29	9	3	5
Number of times trends have occurred	147	27	18	25

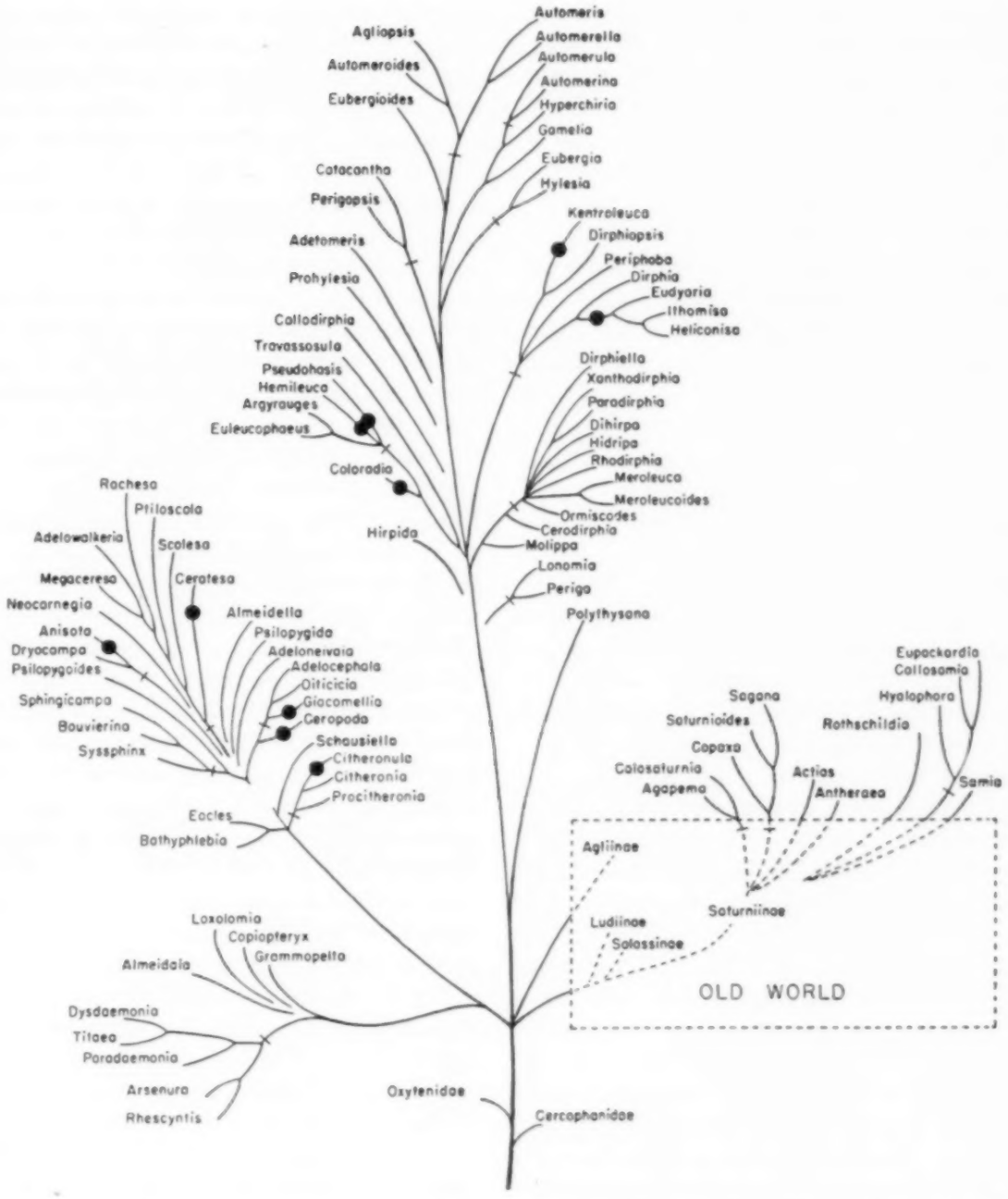

FIG. 8. Phylogenetic tree of the Saturniidae of the New World. The tibiae primitively lack spines. In forms marked by a disk the front tibiae bear at least one strong apical spine.

might have been interpreted as more than one trend, since inner apical spines are not always present, and since the middle tibiae as well as the front ones sometimes have spines. Another structure which seems to be newly acquired is the multiple antennal cone. Apparently each of the distal antennal segments bears, primitively, a single sharp conical projection on its under surface near the apex. In certain groups, instead of a single projection, there is a broad lobe bearing a group of small points. In such groups the antennal cones are termed "multiple." Another minor new structure is a sharp ridge or carina along the under surface of the antenna. This ridge is often produced at the apex of each segment so that simple antennal cones extend nearly to the base of each antenna.

Under "not classifiable" in table 2 are included such trends as that from a large to a small anepisternum. At first sight this would seem to be a reduction, but actually it is merely a change in the course of the anepisternal suture, for as the anepisternum is reduced in size the katepisternum is correspondingly enlarged. In the same category falls the change from nocturnal to diurnal habits. This involves not only the gain of diurnal flight habits, but also the loss of nocturnal ones.

Discussion

The potentiality for similar changes, resulting in parallel characters, no doubt results from the fact that related animals have homologous chromosomes and genes (see Sturtevant and Novitski, 1941). It is evident that certain characters have changed repeatedly in the same manner, while others are relatively stable or changed but once so that the altered feature is regarded as of phylogenetic significance.

Why should certain characters change repeatedly in this fashion? It is well known that in those animals which have been studied genetically mutations occur or at least survive at certain loci more frequently than at others. Mayr and Vaurie (1948) give examples of the occurrence of parallel changes in birds comparable to those here described for the Saturniidae. In these groups, perhaps in all groups, there are much greater potentialities for changes of certain sorts than for those of other sorts. The independent acquisition of, for example, tibial spines in various saturniids may indicate such a predisposition to spined tibiae because of high mutability of a gene locus controlling such spines.

However, as Simpson (1944) has emphasized, there is no necessary relationship between mutation rate and rate of evolution. A high mutation rate at a certain locus might be completely unexpressed in evolution because of the inviability of the mutants. Moreover, there is no certain way of judging whether the presence of spines in various unrelated saturniids is due to separate mutations or is due to alleles common to all or most saturniids but unexpressed in most because of the action of modifiers. Mather (1943) has pointed out that an organism's response to natural selection must depend largely upon stored variability such as this and not upon new mutations.

The significant point is that tibial spines have arisen at least ten times during the course of saturniid evolution. It is certain that selection has played the principal role in determining what variants survive. Simpson (1944) has ably discussed its importance. Both Rensch (1939) and Muller (1939) have pointed out that parallel evolution occurs in animals having similar genetic makeups and subject to similar conditions of selection. In connection with this last point, it is interesting that all American forms having such spines occur in the more or less temperate regions of the United States and Canada or in temperate or nearly temperate areas of southern Brazil, Paraguay, Uruguay, and Argentina. None of the numerous tropical saturniids have tibial spines. So far as known, forms with these spines pupate below the surface of the ground and the spines are thought to be important to the adult in digging its way to the surface. Pupation in the soil is probably one of the ways in which these insects are able to protect themselves from cool winters, although many other northern types survive cold by means of other sorts of adaptations, for they pass the winter as pupae in cocoons hanging in trees.

The remarks already made concerning mutation rates and selection apply equally to the reduction or loss of structures. As Wright (1929, 1940) and Muller (1939) have pointed out, there is considerable mutation pressure against most structures, so that unless they are preserved by selection, they tend to disappear. We must conclude that in at least some groups the selection pressure has relaxed for such structures as the epiphyses, which have been lost at least 10 times (in females) in

saturniid evolution. It is obviously much easier for an organism to lose a previously established character in this way than to acquire a new one. The extent to which this is true is indicated by the numerical data already presented.

A relationship exists between reduced eye size and diurnal habits. Like most moths, most saturniids are nocturnal, but those with reduced eyes are mostly, if not all, diurnal or crepuscular. Perhaps in daylight smaller eyes can perform the functions for which large eyes are necessary at night. Hence small eyes, which would be selectively disadvantageous in most saturniids, are at least not seriously disadvantageous in diurnal forms.

Reduction in eye size is correlated, as already stated, with reduction of other parts of the head capsule; the indication is that this is an example of disharmonic or allometric growth (see Huxley, 1932), the head capsule growing more slowly in relation to the rest of the body than in most saturniids.

Acknowledgments

Grateful acknowledgment is made to Mr. Frank Johnson for the funds made available, both at the American Museum of Natural History where this study was begun and at the University of Kansas. Thanks to his generosity, technical assistants have been available to make dissections and drawings which have aided greatly in the comparative morphological work which is the basis of this study. Doctor Ernst Mayr and Mr. Hewson H. Swift have read the manuscript and offered many valuable criticisms.

Summary

The phylogeny of the Saturniid moths is discussed and several examples are given of independent origin of similar characters in unrelated Saturniids. For example, the loss of a hind tibial spur has occurred independently at least 10 times in one subfamily, of the epiphyses of the female at least 10 times in the family, and of the articulation of the male genital harpes 7 times. Reduction of the labial palpi has occurred at least 9 times, and of the eyes and structures of the head capsule at least 14 times. Large spines are acquired on the front tibiae at least 10 times. A discussion is given of the possible reasons for this extensive series of parallelisms.

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BROMUS INERMIS AND *B. PUMPELLIANUS* IN NORTH AMERICA

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Since the introduction of the grass *Bromus inermis* Leyss. from Europe (Dwinelle, 1884) significant changes have occurred in populations of the North American native *B. pumpellianus* Scribn. This preliminary study is concerned with an evaluation of the apparent introgression of the two species of grasses which has followed. *B. inermis,* grown extensively on ranges and pastures in the United States and Canada, may also be found along roadsides, railroad right-of-ways, and old fence lines rather generally throughout the range as indicated in figure 1. *B. pumpellianus,* the closest North American counterpart of *B. inermis,* ranges northward from the Intermountain Region into Canada and Alaska as far as the Seward Peninsula as indicated by herbarium specimen sources in figure 2. In recent years more aggressive introduced grasses, including *B. inermis,* have largely replaced *B. pumpellianus* and certain other native species in the more fertile areas within the range of the latter.

These two species are the only perennial rhizomatous representatives of the section Bromopsis found in the United States (Hitchcock, 1935). The presence of pubescence on the margins of *B. pumpellianus* lemmas has been employed by several taxonomists as the chief delimiting characteristic. Morphological characters of available material of *B. pumpellianus* and *B. inermis* are shown in figures 3–8.

Taxonomic treatment of this sub-division of the genus by certain authors has revealed the existence of several similar forms from a morphological point of view. Hultén (1942), in his Flora of Alaska, recognizes varieties *arcticus* and *villosissimus* of *B. pumpellianus.* Specimens with pilose glumes and lemmas were classified as variety *arcticus* while those with lemmas covered with dense, villous, gray indumentum were classified as variety

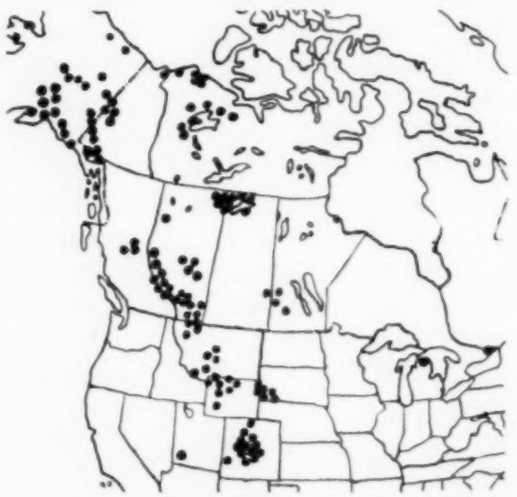

Fig. 2. Distribution of *B. pumpellianus* in North America as indicated by specimens collected during the period 1860–1947. Each dot represents one locality.

Fig. 1. North American distribution of *B. inermis* as indicated by herbarium specimens. Each dot represents a region occupied by the species.

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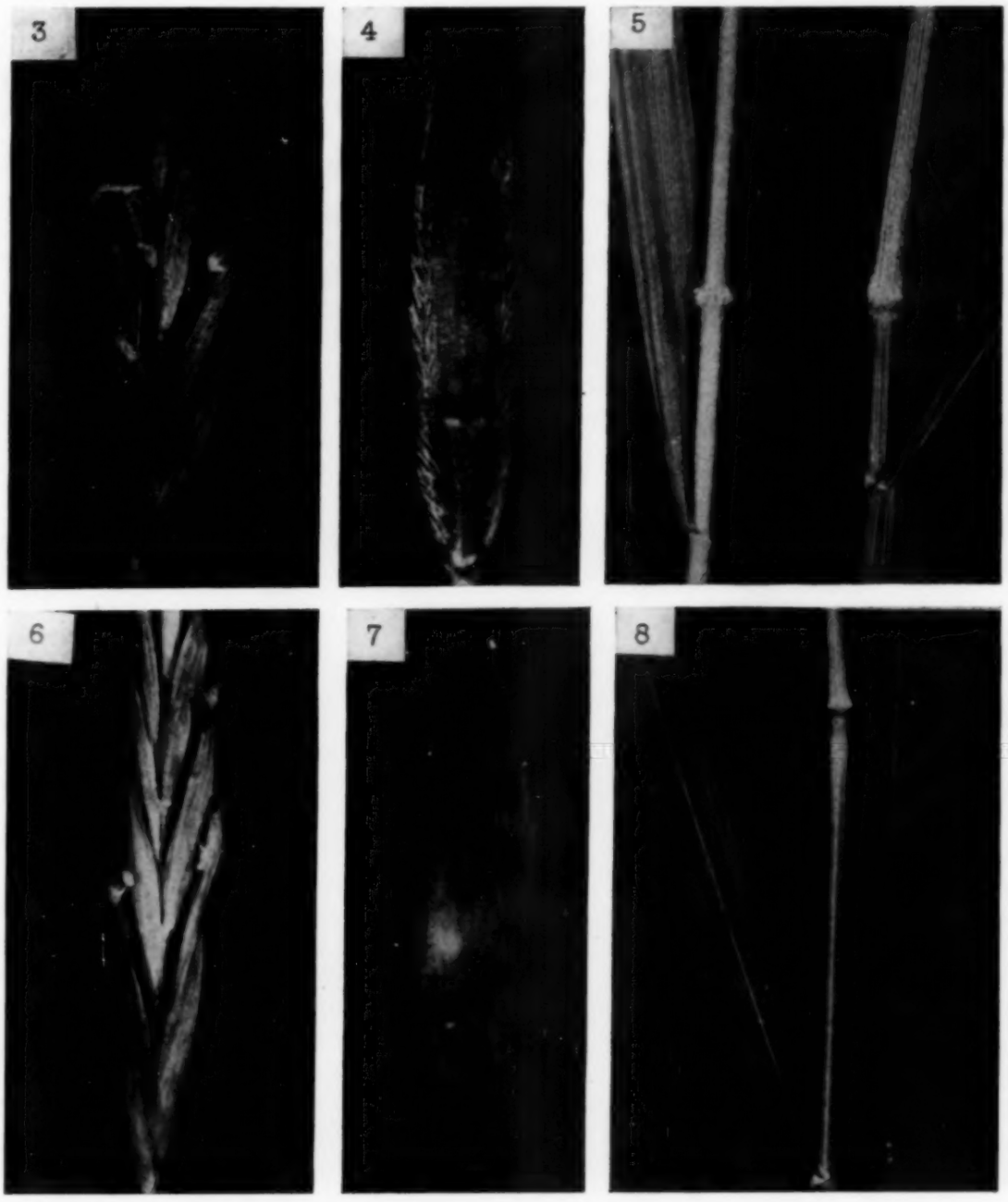


FIGS. 3–5. Spikelet, lemma, and culms of *B. pumpellianus.*
FIGS. 6–8. Corresponding parts of *B. inermis* plants. Note the contrast in pubescence between these species.

villosissimus. He regarded *B. pumpellianus* as closely related to *B. inermis,* differing only in awn length, culm node pubescence, and lemma pubescence. On this basis he postulated that *B. pumpellianus* was the American counterpart of Eurasian *B. inermis* and that its varieties *arcticus* and *villosissimus,* as well as the Kamchatkan *B. ornans,* were northern variations of this complex.

B. ornans, B. korotkyi, B. irkutensis, B. vogulicus, B. richardsonii, and *B. sibiricus,* as treated by Nevski and Sochava (1934), are not sufficiently delimited from a morphological standpoint to warrant exclusion from a complex which would include various forms of *B. pumpellianus.* In their treatment of the sub-genus Zerna *B. ornans* was described as endemic to sandy ridges of river valleys and volcanic

sands on the Kamchatkan peninsula. *B. richardsonii* was described as a rhizomatous perennial with very similar morphology distributed in meadows of eastern Siberia, in Kamchatka, Sakhalin, Udsk, Okhotsk, Zu-Bureya, Ussuria, and also generally distributed in North America, Japan-China (Manchuria) and the eastern part of Mongolia. Hitchcock (1935) reduced *B. richardsonii* to a robust form of *B. ciliatus,* common in the Rocky Mountains, since it graded freely into this species. A robust form of *B. ciliatus* collected in Morain Park, Colorado in 1945 by the author is tetraploid, whereas two collections of this species, one from Maine and one from California, examined by Stebbins (1947) and by the writer, are both diploid. Neither the diploid nor tetraploid forms examined were rhizomatous and cannot, therefore, be regarded as morphologically equivalent to *B. richardsonii,* as recognized by Nevski and Sochava (1934).

B. irkutensis was described by these authors as occurring in the Irkut River valley in eastern Siberia and as generally distributed in Mongolia. *B. korotkyi* is endemic to sandy shores in eastern Siberia and was found on sandy lands along the Ulan-Buri River. *B. sibiricus,* in this flora, was distributed in the northern and central Urals, eastern and western Siberia, and Mongolia. Because of the unavailability of these Asiatic forms for comparative study emphasis in this study has been confined to the species now occurring in North America.

Materials and Methods

Three approaches to the problem were pursued. First, an attempt was made to evaluate the phenomenon of introgression in areas where the two species occur together. Secondly, the specimens of both species deposited with several major herbaria were assembled and studied. The third approach was a study of the hybrids made between plants of the two species. For this portion of the study plants of *B. pumpellianus* from three sources which were as nearly typical as could be obtained were crossed artificially with plants of *B. inermis* growing in the Iowa Agricultural Experiment Station Nursery at Ames.

The Species in Nature

In commenting on the habits of *B. inermis* and *B. pumpellianus* as they are now found in nature at Fort Saskatchewan, Alberta, Dr. G. H. Turner (1946) wrote: "*Bromus inermis,* as we have it here, is very aggressive and now occurs widely and generally in more or less dense stands in any soil where it can obtain a footing. *B. pumpellianus* is very modest in its habits, and remains to be found only on bits of native sod that remain here and there along roadsides, river banks, etc. Usually it is much less caespitose than *B. inermis,* the stems being very discretely spread in such colonies as we have left—*B. pumpellianus* remains easily recognized by its erect panicles and larger spikelets in addition to its pubescence."

In an aspen parkland just off the campus of the University of Alberta, at Edmonton, which has probably been plowed up at least once (Knowles, 1946) the two species also occur together. Among the clones of *B. pumpellianus* obtained from the boundary of an aspen clump were typical representatives of the species. A number of panicles collected from individual clones in several areas throughout the parkland, however, revealed a series of intergrading forms between the two species. It was possible to select a series of mature lemmas from plants in the area intergrading from the more or less glabrous lemma condition characteristic of *B. inermis* to dense, marginal pubescence typical of *B. pumpellianus.* From these and other available sources a series of model lemmas were selected and assigned pubescence values from 1 to 8 (see fig. 9). Lemmas of 0, 1, and 2 value were arbitrarily considered *B. inermis* while classes 6, 7, and 8 were designated *B. pumpellianus.* Type specimen material of the latter examined, however, was of class 6 lemma pubescence.

Forms of this species from Alaska, Yukon, and the Northwest Territories had more extreme pubescence and were assigned class values of 7 and 8.

The Herbarium Specimens

Several hundred herbarium specimens of *B. inermis* and *B. pumpellianus* collected in various North American localities over a 90 year period were scored for lemma pubescence. Their distribution is presented in figure 10. A number of intermediates were encountered which are represented in classes 3, 4, and 5 of figure 10. Between 1895 and 1900 intermediates were collected in Colorado, Montana, and Alberta (see fig. 11). During this same period *B. inermis* became established in numerous hay and pasture seedings throughout the Intermountain Region. An intermediate lemma pubescence was also found in certain specimens collected later from Minnesota, Wisconsin, Connecticut, and Quebec which are, supposedly, outside the known range of *B. pumpellianus*. In the Intermountain Region the intermediates were often collected in artificially modified habitats such as roadsides, highway shoulders, and railway embankments. The distribution of the

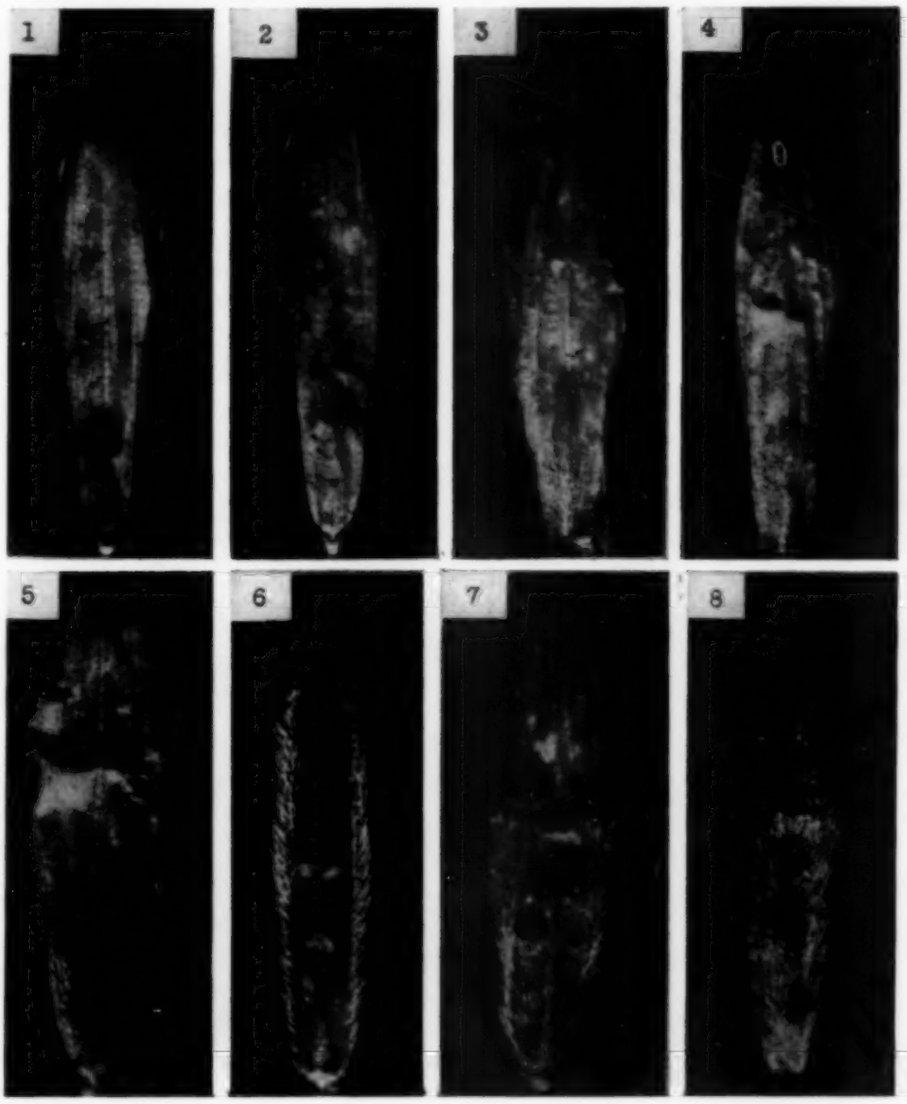


Fig. 9. Pubescence of model lemmas selected among plants of *B. inermis* (1 and 2), *B. pumpellianus* (6, 7, and 8), and naturally occurring intermediates (3, 4, and 5).

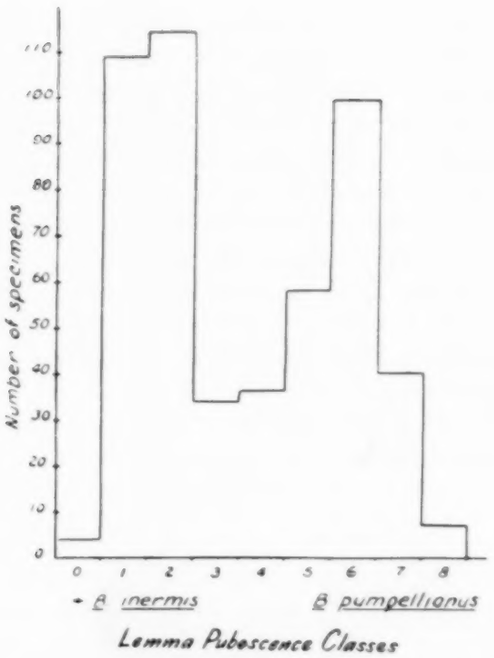


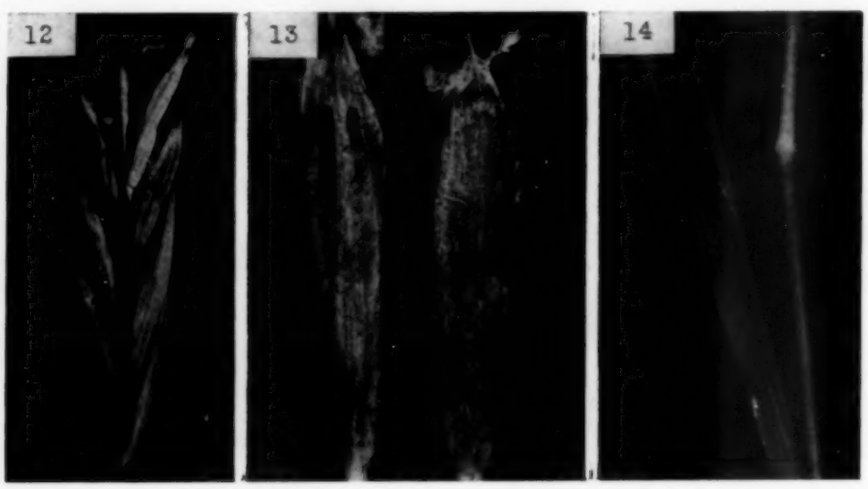
FIG. 10. Distribution of lemma pubescence classes among 501 North American specimens of *B. inermis* and *B. pumpellianus* collected in the period 1860–1947.

intermediates in eastern United States and Canada was, without exception, in terminal moraine areas.

THE SPECIES HYBRIDS

As indicated elsewhere (Elliott, in press) the average cross-fertility obtained between plants of *B. inermis* and *B. pumpellianus* was approximately half that obtained in intraspecific matings of both parental species. Certain interspecific matings, however, were as highly cross-fertile (as expressed by per cent seed set) as some intraspecific crosses. The F_1 hybrids were generally intermediate but not at all uniform in morphological characters. Some hybrids possessed lemma pubescence more nearly approaching *B. pumpellianus* (see figs. 12–14) than the intermediate condition. However, somewhat less pubescent backcrosses or other complex hybrids with *B. inermis* might be encountered more frequently in nature than actual F_1 hybrids. It was impossible in this pre-

FIG. 11. North American distribution of intermediate lemma pubescence (classes 3, 4, and 5) from herbarium specimens. Each dot represents one locality.



FIGS. 12–14. Spikelet, lemmas, and culm node of certain F_1 hybrids of *B. inermis* × *B. pumpellianus*.

liminary study to determine the degree of heritability for lemma pubescence in view of the variable and heterozygous nature of the parents. The seed-setting fertility of the F_1 hybrids under study was observed to range from 14% to 33% from open-pollination in the greenhouse, while typical *B. inermis* plants in the same experiment ranged from 13% to 59% seed-set.

Discussion

The geographical distribution of the intermediates shown in figure 11 would suggest that hybridization of the two species under study occurred in a number of locations before the turn of the present century. Indeed, on the basis of the specimens examined, it can be reasonably postulated that hybridization is still occurring between the two species in numerous areas within the range of *B. pumpellianus*. In addition to the Edmonton, Alberta parkland previously mentioned, the Waterton Lakes parklands, Alberta, and certain locations in the Black Hills, South Dakota, yielded a considerable number of intermediate specimens of recent collection. There are evidences of many other isolated areas where hybridization has probably occurred in recent years. In view of the known range of *B. pumpellianus* the existence of the intermediates in Minnesota, Wisconsin, Connecticut, and Quebec is subject to some speculation. In the writer's opinion their presence is evidence, although still inconclusive, that relic populations of *B. pumpellianus* may have been, or still are, distributed in eastern United States and Canada in the areas from which the intermediates were sampled. Hitchcock (1935) considered the Michigan *B. pumpellianus* an introduction. This interpretation is questioned in view of the Canadian and American distributions of the intermediates as well as typical *B. pumpellianus*. The following species of seed plants have been reported by Fassett (1941), Munns (1938), Hopkins (1937), Hitchcock (1935) and Marie-Victorin (1938) to have North American distributions similar to those noted for *B. pumpellianus:*

Rubus parviflorus, Populus balsamifera, Picea glauca, Arabis divaricarpa, Scirpus pumilus, Listera borealis, Antennaria pulcherrima, Festuca scabrella, Poa interior, Poa alpina, Poa canbyi, Melica smithii, Agropyron bakeri, Agropyron spicatum, Deschampsia atropurpurea, Danthonia intermedia, Calamagrostis neglecta, Phleum alpinum, and *Orysopsis asperifolia.*

For the present, at least, the possibility of the observed intermediates representing extreme variants within *B. inermis* is discounted since they should also have been found as often in other localities of comparable latitude and soil conditions sampled equally as well. As previously noted, their distribution in this general area was, without exception, in terminal moraine areas where stony habitats presented a minimum of floral competition. In the terminal moraines or high rocky habitats chance recombination products with *B. pumpellianus* characters would not have been critically selected against. So long as effective asexual propagative characteristics were maintained the reduced fertility of the hybrids need not have been a critical factor. Because of a general lack of aggressiveness *B. pumpellianus* has not been able to compete with *B. inermis* in the more fertile mountain valleys where it once was, apparently, much more plentiful.

The moderate fertility of hybrids between *B. inermis* and *B. pumpellianus* is suggestive of a rather recent migration, as regards geological time, from a geographical center which was a common source of germplasm. This migration most logically took place from the direction of Asia. It is expected further that this extensive migration occurred in a Pleistocene era when cool moist conditions prevailed over a large area of North America. The now widely separated endemic distribution of *B. pumpellianus,* for example, is confined to reasonably cool and moist habitats. It would appear that

some additional mechanism, geographical or otherwise, was operative in restricting the variability of the population of this complex gaining access to the North American continent. Or, having reached the continent, the most recent glaciation so reduced the effective breeding populations that inbreeding and serious depletion of variability followed. Some hypothesis of this nature seems necessary to account for the apparent failure of *B. pumpellianus* to maintain confluency of distribution over an area where *B. inermis* is particularly well adapted.

The absence of well-defined reproductive barriers between *B. inermis* and *B. pumpellianus* has prompted the question of specific validity. Since the geography of North America and Asia served as the main isolating mechanism of the two species, it seems appropriate to reduce *B. pumpellianus* to at least a race (subspecies) (Dobzhansky, 1941) of *B. inermis*. From the standpoint of nomenclature the distinct sub-species diagrammed by Clausen, Keck, and Hiesey (1939) is probably applicable to *B. pumpellianus*.

Significant changes have most certainly occurred in populations of both species since the introduction of *B. inermis*. The alterations of natural competitive relationships imposed by increasing acreages of *B. inermis* are difficult to enumerate. Since the two are neither comparable from the standpoint of population frequency nor competitive ability, detailed analyses of their introgression are complex.

Introgression has probably occurred as the result of the introduction of numerous cross-pollinated grasses whose North American counterparts were isolated similarly to *B. pumpellianus*. Within the genera *Festuca, Poa, Agropyron, Calamagrostis,* and *Phleum* there are a number of possible examples. Innumerable transfers of genes from the native forms, although perhaps not of comparable vigor or productiveness, have, thus, been possible. In many important forage grasses introgression may have aided in the establishment of types more favorably adapted to specific environments.

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Summary

The distributions of native *Bromus pumpellianus* Scribn. and the introduced forage species *B. inermis* Leyss. in North America are outlined. Evidence is presented for the introgression of the two within the range of *B. pumpellianus*. Hybridization of the two appears to have largely taken place in artificially modified habitats. The known range of *B. pumpellianus* is extended to account for the distribution of forms with intermediate lemma pubescence in eastern United States and Canada. F_1 species hybrids were moderately fertile as indicated by percentage seed set under open-pollination. Recent divergence of the two species from an Asiatic center of germplasm is suggested. In view of the emphasis upon the geographical nature of the isolating mechanism involved, *B. pumpellianus* might well be reduced to a race (subspecies) of *B. inermis*. Introgression is postulated within several grass genera where cross-pollinated, introduced species have met similarly isolated North American counterparts.

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AVIAN RELICTS AND DOUBLE INVASIONS IN PENINSULAR INDIA AND CEYLON

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One of the most interesting evidences of speciation is in connection with double invasions. Double invasions occur when two closely related populations arrive in an isolated area at different times. For some reasons, genetic and ecological, they are able to maintain their separate identity and coexist without interbreeding. A number of such cases, particularly for oceanic islands or other isolated areas, have been cited by Mayr (1942).

Double invasions are more difficult to study on or about continental areas. Here auxiliary factors must play their part in order to create the necessary isolation. Geological changes may occur and in their wake bring secondary ecological shifts. The peninsula of India and the island of Ceylon are such areas, and I have been able to collect specimens and study the faunas of both places during the war (Ripley, 1946), and during the winter of 1946–47.

The peninsula of India and Ceylon have long been noted for their peculiar and isolated faunas. Salim Ali (1935) has made an interesting survey of the south Indian states of Travancore and Cochin, in which he points out the similarities of the fauna of these states to that of Assam, Burma, and Malaysia, over a thousand miles away. He describes the climatic similarities of the two zones, separated by a relatively arid intervening area. Earlier authors, noting the close resemblance of the faunas of these zones, had suggested that a bridge of some sort must once have existed between south India and Ceylon and the Malay peninsula. Recent work tends to discredit this land-bridge thesis and to look instead for the explanation in recent physiographic changes in peninsular and central India.

There are three main factors which have created the isolated biota of south India and Ceylon. The first is geologic. By Pliocene time the main backbone or watershed of India, as Wadia (1944) calls it, had arisen. This consisted of the Vindhyan Hills and the Kaimur Ridge running east to Rajmahal, across the gap of alluvial deposits connected with the present course of the Ganges and Brahmaputra rivers, and on to the Khasia and other central hill ranges of Assam (fig. 1). This mountain chain undoubtdely served as a faunal link between the mountains of southwest peninsular India and the Himalayas, a bridge by which the forms of one area could be dispersed continuously throughout the other.

There has been considerable recent discussion on the age and configuration of the Rajmahal gap alluded to above, as it provides an important break in the backbone. Hora (1944) postulates that the gap was formed in mid-Miocene time, was closed in Pliocene time by block-faulting, and finally reopened in the Quaternary. He maintains that such a series of events would have had to occur in order to allow for the migration of freshwater torrential fish from Assam into the peninsula. Aside from these torrential fish, whose potentialities for secondary adaptation are not considered in Hora's paper, I would assume that the majority of the flora and fauna which had migrated from the north would be able to cross the Rajmahal gap during the pluvial periods. Presumably the gap was much narrower in late Tertiary or early Quaternary time, and in the absence of any sound geological evidence to the contrary, it would seem wiser to assume that it has existed continuously since its formation. The

FIG. 1. Map showing elevations in south India and in Ceylon which capture southwest monsoon rains, and probable route across the central Indian hills by which relicts and double invasions arrived from the Himalayan and Indo-Chinese subregions.

narrowness of the gap in the beginning of the Pleistocene is attested by the drainage system which only then became split. It was at this time that the Brahmaputra was captured by the Teesta and the lower Ganges rivers and diverted away from the westward-flowing Indobrahm system.[1]

In connection with the above, it is worth pointing out that care must be exercised in zoogeographic discussions of the Indian peninsula, which is sometimes thought of as a sort of heartland for the old Gondwana continent. Voous (1947, p. 130), speaking of the origin of the woodpecker, *Dendrocopos mahrattensis*, says that the Tethys Sea isolated peninsular India from the rest of Asia during the Pleistocene. Actually the Tethys Sea, as such, was a Mesozoic feature which had disappeared by the beginning of the Tertiary.

The second main factor is climatic. The pluvial epochs, which Blanford (1901) first discussed, have undoubtedly had an important effect on the dispersal of Himalayan-affinity flora and fauna into peninsular India. With the lowering of the temperature and increased humidity correlated with the advance of the glaciers, a tremendous impetus would be given to accidental dispersal and spread of montane

[1] For further discussions of these epochs, see Wadia (t. c.), de Terra (1934), and others. Unfortunately there is no survey of the Pleistocene in India comparable in any way to Zeuner's studies for Europe.

forms. Successions of such epochs, with relatively warm and arid phases between, would presumably allow for more than one invasion of the area.

The third factor, of course, is that the elevation of the hills along the Malabar coast and in Ceylon is sufficient to capture the necessary monsoon rains to create "evergreen" or rain forest conditions. Rainfall in this region at present ranges between 75 and over 100 inches per annum. As a result, the western faces of the southwest Indian hills and the hills of Ceylon have become ecological "islands."

The general climatic correlation to be derived from the above is one of alternating cycles during the glacial periods. Periods of low temperature and increased humidity would allow montane species to spread south from the Himalayan axis, only to be isolated eventually by the succeeding periods of higher temperatures and increasing desiccation. Thus what may be termed pluvial relict species have resulted in a number of cases. An additional development has been the arrival of secondary and even tertiary waves of immigrants in the peninsula and in Ceylon, thus creating double invasions. In all the cases reported on in the following sections, these secondary immigrants have become adapted to changed climatic conditions, and have been able to spread throughout the more desiccated areas. In most cases the primary immigrants have remained adapted to the humid evergreen forest conditions. However, in two cases I believe that two waves of immigrants have arrived during dry periods and that the interval between their arrivals has been sufficient to permit the development of isolating mechanisms. De Terra and Paterson (1939, p. 316) note that the climate of central India had already become "dry-tropical" by mid-Pleistocene time.

Randhawa (1945) states that there is evidence that desiccation in the northern part of the Indian peninsula is increasing rapidly. He believes that in the last 2000 years there has been a very marked reduction in rainfall and a consequent change in the composition of the forests. He cites numerous records of formerly abundant forest types to emphasize his point. Thus the climatic and ecological pressure on the fauna is increasing in intensity.

Relict Forms

Following is a list of the avian relicts in south India and Ceylon which have become isolated as a result of the factors enumerated above. Plant relicts have been discussed by Pearson and Brown (1932). Hora (1944) lists the most recent discoveries among the fish. There are no comprehensive lists in this or any other class of animals. Among the mammals there are two outstanding relicts: *Hemitragus nilgiriensis,* the Nilgiri tahr, found in south India but not in Ceylon, and *Martes flavigula,* a marten, found in Ceylon and south India.

Avian Relicts

1. Species identical in both south India and Ceylon.

Species	Affinities
Aviceda l. leuphotes	Himalayan
Aviceda jerdoni ceylonensis	Himalayan
Batrachostomus moniliger	Himalayan
Irena p. puella	Himalayan

2. Species with differing subspecies in both areas.

South India	Ceylon	Affinities
Bubo n. nipalensis	*Bubo n. blighi*	Himalayan
Zoothera d. neilgherriensis	*Z. d. imbricata*	Himalayan

3. Superspecies with different species in both areas.

South India	Ceylon	Affinities
Gallus sonnerati	*G. lafayetti*	Himalayan
Columba elphinstonii	*C. torringtoni*	Himalayan
Psittacula columboides	*P. calthorpae*	Himalayan
Loriculus v. rubropygialis	*L. beryllinus*	Himalayan
Pycnonotus gularis	*P. melanicterus*	Himalayan
Muscicapa albicaudata	*M. sordida*	Himalayan
Sturnus m. blythii	*S. senex*	Himalayan

4. Species present in India, absent in Ceylon.

Species	Affinities
Eurostopodus m. bourdilloni	Assam
Chaetura g. indica	Himalayan
Nyctiornis a. athertoni	Himalayan
Buceros bicornis	Himalayan
Dinopium j. malabaricum	Malaysian
Hemicircus c. cordatus	Assam
Dryocopus j. hodgsonii	Burma
Vivia i. avunculorum	Himalayan
Brachypteryx major (2 subsp.)	Himalayan
Myiophoneus horsfieldii	Himalayan
Garrulax cachinnans (5 subsp.)	Himalayan
Garrulax delesserti	Himalayan
Muscicapa nigrorufa	Malaysian
Arachnothera l. longirostris	Himalayan

5. Species absent from India, but present in Ceylon.

Species	Affinities
Phaenicophaeus pyrrhocephalus	Malaysian
Megalaima flavifrons	Malaysian
Pycnonotus penicillatus	Assam
Zoothera spiloptera	Malaysian
Myiophoneus blighi	Malaysian
Pellorneum fuscocapillus (3 subsp.)	Assam
Garrulax cinereifrons	Assam
Bradypterus palliseri	Malaysian
Dicaeum vincens	Himalayan
Kitta ornata	Himalayan

The above list includes 44 species. The additional double invasions are listed later. It is interesting to note from the above that the relicts found only in Ceylon (category 5) are the most isolated, that is, their relatives are the farthest away geographically at the present time, 80 per cent having only Assam or Malaysian affinities.

The name "relict" applied to some of the above might be questioned. I would define a relict, in this geographical and not phylogenetic sense, as a population which has become isolated from its nearest relatives by some geological or climatic change. Its very presence in an area tends to appear anomalous and to draw attention to possible environmental changes.

The two species of *Gallus* would seem to be isolated relicts of previous invasions of *Gallus* stock in peninsular India and Ceylon. Sonnerat's jungle fowl does occur right into central India, and in that area hybrids occur with *Gallus g. murghi* (specimens in Koelz collection). I would hazard, however, that this contact is uncommon and relatively recent.

The trogon, *Harpactes fasciatus,* occurs from the south Indian hills of Travancore and Cochin north along the Western Ghats and apparently sparingly east along the chain of hills to Chota Nagpore and extreme western Bengal. The northern limit of its distribution, therefore, occurs along the line of immigration from the Rajmahal gap as postulated. The starling species, *Sturnus malabaricus,* is included, as recent evidence (Whistler and Kinnear, 1933) would indicate that the nominate race breeds up into the Himalayan foothills and not in peninsular India.

Statistical Analysis

Attempts on my part to derive correlations or associations based on these data have been unsuccessful. The actual number of cases is small, and there are none but the most arbitrary methods of attempting to correlate the figures for the fauna against the geographic or geological factors. The number of resident avian species in the Himalayas comes to about 432; those in south India 235, and in Ceylon 175. Thus there is a decline of 46 per cent and 60 per cent, respectively, in the resident population of the two areas. The number of double invasions in south India is 5, and in Ceylon is 7. By Chi-square tests these figures and those of the endemisms and relict species seem to vary independently. It would be interesting to know whether there is any correlation between the occurrence of double invasions and the progressive isolation and decline in numbers of a fauna, but the available data do not permit a quantitative consideration of the matter.

Double Invasions

In the following discussion I have listed a total of 9 double invasions of south India and Ceylon. These cases may be di-

vided into two principal categories, as follows:

(A) those species in which reproductive isolation is not yet established, and
(B) those species in which reproductive isolation is established.

Under Type (A) in the following pages I have listed three species whose representative subspecies in the peninsula and Ceylon are largely allopatric. The reader may question my decision as to why these species represent double invasions. Why could they not simply be relict species which have fanned out into different local environments and developed recognizable subspecies? This has happened in three of the relict species listed under categories 4 and 5 in the preceding discussion. A robin and a babbler that are widespread in south India, *Brachypteryx* and *Garrulax,* have developed different subspecies within the rainfall areas of the western side of the peninsula. Again, in Ceylon a babbler, *Pellorneum,* has developed three subspecies in both dry and wet zones.

My reasons for considering the three following cases to be double invasions have been twofold. In the first place, in each of the double invasions listed hereafter there is an ecological preference of one form for damp evergreen jungle. A species found in damp evergreen jungle in this area is a relict as defined previously. Consequently it is an earlier arrival than a species found in the drier areas. Added to this is the fact that in each of the following cases of Type (A), the external differences between the forms, the partners of the double invasions, are very great, far greater than those normally encountered among neighboring subspecies of a species. From the taxonomic point of view these forms were formerly considered good species because in appearance they were so markedly different. However, in two cases hybrids have been discovered between the forms in areas of range contact and in the third case there is no evidence to indicate that the ranges are not strictly allopatric. Modern taxonomists, therefore, would have no hesitation in listing all these forms as members of the same species. But at the same time these taxonomists would agree that the external differences between the forms imply a very long period of isolation.

When applied to Type (B), those species in which reproductive isolation is established, I believe that the earlier species is the one which inhabits the damp evergreen jungle. It is presumably a relict. In the same way an isolated species, one without close relatives in near geographic areas, is of course a relict. If such a species without developing subspecies is found in the same area with another species which is related to it, and if this second species has developed many subspecies and covers a wide area throughout southeastern Asia, then I would feel (*contra* Willis) that the first species is the earlier arrival.

Type (A).

1. *Glaucidium radiatum*

This owl has reached south India and Ceylon twice, and the resulting populations are presumably allopatric. In south India there are two races. The earlier, *malabaricum,* is a very dark type confined to the deciduous forest, low country, and foothills to 2500 (once 4500) feet, of Travancore and Cochin. The later immigrant, *radiatum radiatum,* is found generally throughout the deciduous biotope of the foothills to the east and north of the range of the former.

In Ceylon there are two races, *castanonotum,* the earliest, being found in the low country evergreen forest, the wet zone of the southwestern part of the island, and in the hills to 6300 feet. This race is so markedly different in appearance that it has been listed as a separate species, or as a member of a closely allied species of the Indo-Chinese subregion, *cuculoides,* by earlier taxonomists working with limited material and distribution evidence. Actually it is a very strongly differentiated form of *radiatum,* its appearance implying long isolation. The second inhabitant is

typical *radiatum radiatum,* found throughout the rest of the island. The fact that *r. radiatum* occupies the drier areas of peninsular India and Ceylon as one identical population would imply a rather recent date of arival in the area. The fact also that *malabaricum* is merely a good subspecies of *radiatum,* whereas *castanonotum* is so well marked as to have caused wide divergence of opinion among older taxonomists, suggests a triple invasion by *radiatum* stock of the area.

2. *Dinopium benghalense*

This woodpecker species has two races which inhabit south India and show an ecological preference implying a double invasion. The darkly colored, distinct race, *tehminae,* is found in the lightly wooded lowlands up to 2000 feet of the humid area of the peninsula in Travancore and Cochin. The other race, *puncticolle,* is widely distributed in central India and the peninsula in the drier areas exclusive of the Malabar coast.

In Ceylon again there are two races, the earliest, *erithronothon,* being found generally throughout the low country up to 4000 feet, except in the northern most desiccated part of the island. This race is very distinctively marked, having a completely saturated back, colored dark reddish, rather than the yellow or golden-yellow tint shown by the other races. In the northern dry zone a race, *jaffnense,* occurs, only slightly differentiated from the Malabar race, *tehminae.* This is the race formerly called *Brachypternus intermedius,* cited by Mayr (1942, p. 173) as an example of a double invasion. The area of contact of the two Ceylon races shows a wide zone of intergradation. If it is reasonable to suppose that hybridization has not *always* occurred between these two populations, then one must assume, I believe, that *erithronothon* represents the earliest wave of arrival, followed later by a second *tehminae-jaffnense* wave; and lastly, and relatively recently, a third population, *puncticolle,* has arisen which is now resident in widespread areas of central India and the peninsula.

There is little evidence as to the success or failure of the hybrid population in Ceylon. Hybrid individuals merely show a blending of the back colors. Specimens are too few to indicate any sorting out of characters.

3. *Dissemurus paradiseus*

The racket-tailed drongo is found in two well-marked races in Ceylon. One, *D. p. lophorhinus,* the earlier arrival, occurs in the evergreen wet zone of the southwest up to 4500 feet. It lacks the conspicuous racket tail feathers and the strongly developed and recurved forehead plumes of typical *paradiseus.* In these characters it approaches other forms widely separated from it geographically, but found at comparable latitudes in the Andaman Islands and Malaya. It thus differs considerably from the races of *paradiseus* found in the rest of Ceylon and in India. The race, *D. p. ceylonensis,* with well-developed rackets and recurved forehead plumes, has evidently arrived later, differing but little from its Indian relatives. This race occupies the drier areas of the island.

It has been suggested that the *lophorhinus* stock might have arrived in Ceylon by a different route than down the peninsula of India, in other words, across the Bay of Bengal from the Andamans or Malaya. I am reluctant to accept this thesis based on phenotypical resemblance. I would feel rather that the resemblances are due to the persistence of old alleles for the following reasons: the southwest monsoon being the dominant factor in the area, approach to Ceylon from the east or northeast becomes even more unlikely for these birds whose range is otherwise confined to nonoceanic islands close to or on continental shelves; the rest of the resident species of Ceylon do not lend themselves to such a transoceanic immigrant theory, but, on the contrary, several other parallelisms exist, viz., *Surniculus, Caprimul-*

gus, and *Spilornis,* all of which resemble Malaysian relatives; and finally, *D. p. lophorhinus,* although not closely resembling *ceylonensis,* hybridizes with it under wild conditions. These hybrids cannot be rare for they were collected by Legge over 70 years ago as well as by myself in 1945. Although we do not know the degree of viability of these hybrids, is it not reasonable to assume that the two parent forms are more closely related than they presumably would be if they were immigrants from two widely separated sources?

As in the woodpecker, the racket-tailed drongo seems to be a well-marked double invasion which has a zone of hybrid overlap.

Type (B).

4. *Centropus*

In Ceylon there has been a double invasion by two species of ground cuckoo or "coucal." These species have apparently achieved reproductive isolation, although they are closely related to each other. The earlier species is apparently *chlororhynchus,* which is found in the low country evergreen forest of the wet zone and into the hills to 2500 feet. It hugs dense forest. This is an endemic species, found only in Ceylon. The second wave consists of *sinensis parroti,* common to all zones, but partial to deciduous scrub jungle. *C. s. parroti* occurs also throughout peninsular India. In size and appearance the two species are extremely similar except for the bill of *chlororhynchus,* which is chartreuse green in color whereas that of the other coucal is black. From the evidence it would appear that the species are sympatric in a geographical sense but are ecologically isolated due to their differing habitat preferences. However, the recent reduction of evergreen forest in southwest Ceylon has been so great that it is questionable whether these habitat preferences can still apply. If, then, these species are not ecologically isolated at present, the distinctive bill character is presumably a factor in preventing hybridization.

5. *Megalaima*

Two species of barbet, obviously closely related, are found both in south India and Ceylon. One is an endemic relict, *M. rubricapilla,* apparently the earlier arrival in the area. There are two well-marked races. One, *malabarica,* occurs in the evergreen biotope of southwest India, from the lowlands up to 4000 feet. The other race, *rubricapilla,* is found in the low country and up to 4000 feet in Ceylon, primarily in the wet zone. The second species, *haemacephala,* apparently a recent arrival and most closely related to *rubricapilla,* has one race, *indica,* found in both areas in the drier zones, primarily in low country, but in Ceylon up to 3000 feet. *M. h. indica* occurs over most of India and into southeastern Asia.

There is a considerable margin of overlap in area between the two species in Ceylon. I have seen both species in a single tree in the central and southeastern parts of the island. These behave like good species, and differ distinctively in color pattern, presumably a sufficient isolating mechanism. However, they seem to be partially sympatric, are identical in size, and have identical food habits. Lack (1944, p. 282) stipulates that under such conditions some sort of pre-adaptation from the ecological point of view must exist. In this particular case my only observation has been that these barbets are always sparingly distributed. Some external factor aside from food may operate here to limit the populations.

6. *Turdoides*

These babblers must be listed under Type B. Their distribution and ecology are most perplexing. One species, *sommervillei,* has broken up into several races in central and south India. It is a fairly wide-ranging species found across central India. It occurs in deciduous scrub and bamboo forest as well as in gardens and near cultivation. A second relict species, *striatus,* is found only in Ceylon and with a separate race, *affinis,* in peninsular India. This species occurs in low country

and is slightly more tolerant of dry conditions. It is found in more open situations as a result and occurs even more frequently in gardens and near habitations. Neither species has a well-defined breeding season. Both species are virtually identical in size and coloration. One, *striatus,* has a tendency to a paler head and a slightly shorter, more arched bill. Both species have similar food habits and, except for the slight difference in climatic preference which seems to operate only on the fringes of their respective ranges, are completely sympatric. They have been observed associating in the same flock on numerous occasions.

In Ceylon there is again a double invasion. The earlier immigrant, *rufescens,* which I was at first inclined to put in *sommervillei* (1946, p. 222), seems to me better left as a species for the following reasons: it is a very dark rufous form, more distinct than any other of its relatives, and in shape of bill and character it seems to me very much an intermediate, if such can be said to exist between such closely similar forms, between *sommervillei* and *striatus.* The species *rufescens,* then, occurs in southwest Ceylon in the low country wet zone and into the hill zone in evergreen jungle. The other resident of Ceylon is *striatus striatus* which occurs in all zones. It differs from *rufescens* in paler coloration (to make the position more difficult, worn specimens of *striatus* often become very reddish) and in possessing a wing-tail index of less than 100 percent. Again, as in the Indian species, both forms may on occasion be seen flocking together.

In both areas it is difficult to see how the existence of these species is maintained genetically or ecologically. And yet no hybrids are known among these forms, and the species continue to occur side by side. Possibly the lack of hybrids may be correlated with some as yet unobserved behavioral difference between the species. A clue may lie in the very close flock pattern of behavior in which family parties stay together in a manner reminiscent of the geese. From the ecological point of view, slight differences in habitat preference may serve to maintain a population reservoir sufficient to guard against extinction of either one of the species, although, in the case of the Ceylon *rufescens,* it would seem as if its habitat was almost totally invaded and swamped. However, *striatus* may still be appreciably less tolerant of the humid evergreen zone preferred by *rufescens.*

7. Gracula

In Ceylon two mynah species occur, *G. ptilogenys,* the earlier arrival, occupying the low country wet zone and hill zone. This endemic species, found only on the island, is very distinct, lacking the double head wattle of its congener, and also being somewhat larger. The other species, *G. religiosa indica* of India, Burma, and Ceylon, seems to be a relatively recent undifferentiated immigrant which is found predominantly in the low country. Both species are known to occur in the low country wet zone without hybridizing, but whether or not this is a recent phenomenon is unknown. It could be recent, due to the gradual disappearance of the primeval forests of the island under the stress of cultivation and lumbering operations. Not enough information is at present available to attempt to determine the degree of ecological pressure between the species. As in the case of the babbler, *Turdoides s. striatus,* there is a possibility that *Gracula religiosa indica* is less tolerant of evergreen forest and a 75-inch rainfall than is *ptilogenys,* and this factor may serve to protect the latter species from being totally swamped.

8. *Zosterops*

Two closely related white-eye species are found in Ceylon. One, the endemic *Z. ceylonensis,* the earlier arrival, occurs in the hill zone. The other, *Z. palpebrosa egregia,* the Ceylon race of a widespread Indo-Malaysian species, is a low country and foothill form. It is somewhat smaller and paler than *ceylon-*

ensis. The two species overlap from about 1500 to 3000 feet. They presumably have the same food habits. The breeding season is the same, but no hybrids are known. Both forms behave like good species.

9. *Dicaeum*

Two flower-peckers occur together in south India. One, *D. erythrorhynchos,* the earlier arrival, has a race in Ceylon. It is a relict species found only in peninsular India and in Ceylon. In south India it is a low country bird not occurring over 2500 feet, while its representative in Ceylon is found at the highest elevations. The other wide-ranging Indo-Malayan species, *concolor,* presumably a later arrival, occurs from the low country to 4000 feet in deciduous and mixed deciduous-evergreen types. It is not found in Ceylon. Of the two, *concolor* is slightly darker with a slightly larger bill but both are startlingly similar and closely related; *vide* Mayr and Amadon (1947). Both species have the same food habits, being largely dependent on various parasitic berry-bearing plants such as *Loranthus.* Both species may be found together on the same plants and are almost indistinguishable on the bush or in the hand. Their call notes are said to be slightly different, implying behavioral differences which may help in preventing hybridization. From an ecological point of view it is again difficult to see how two species with such similar habits can coexist. Here again the key may lie in the slight observed differences in habitat preference, tending to preserve a reservoir of the two species on the fringes of their ranges in isolation from each other.

Discussion

Lack (1944), discussing the ecological aspects of species formation, concludes that when two forms, differentiated in geographical isolation, later meet in the same area, two species will result and will persist only under two given conditions. Firstly, the two forms must be sufficiently different genetically not to interbreed freely, and secondly, they must be sufficiently different in their ecological requirements to avoid too severe competition with each other. In the cases listed under (A) above, there is little, if any, pressure. Under (B), however, there are several cases which are puzzling. Lack (l.c., p. 276) suggests the theoretical possibility that if the limiting factors tending to control the numbers of two species operate solely outside the breeding season, the species may be able to mix freely when breeding. Similarly the converse may be true should two species mix only in the non-breeding season. In most of the cases listed there is little or no evidence for decided shifts of range during the breeding cycle on the part of one of the pair of forms. However, the mere fact that these are cases of double invasion alleviates the more basic problem of the actual speciation process involved, as discussed by Mayr (1947). All these species apparently evolved in geographic isolation and have become sympatric secondarily through an extension of range.

Thorpe (1945) postulates speciation occurring by the evolution of habitat preferences. In these Ceylon and south Indian sympatric species it seems unnecessary to depend on this theory. Rather the features listed earlier would seem to allow for an ideal development of double invasions. The isolation of the area is due to the tenuous nature of the link, the bridge of hills running down from the Himalayas. The sequence of pluvial and interpluvial periods has induced a whole series of widely varying ecological conditions. Finally, the present climatic conditions have succeeded in preserving, in two "islands," a host of relict forms. Without such relicts, double invasion would not be otherwise apparent.

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Summary

A discussion of the geological and physiographic factors influencing south India and Ceylon indicates that conditions there have been ideal for the development of ecological "islands." Given these islands and a succession of climatic epochs correlated with the glacial periods, numerous pluvial relicts have evolved. In addition, nine cases of presumed double invasions are known. These examples of double invasion have been divided into two types, depending on whether or not reproductive isolation has yet been established. Three of these cases, the owls, *Glaucidium*, the woodpeckers, *Dinopium*, and the racket-tailed drongos, *Dissemurus*, fall into the first category in which reproductive isolation is presumed or, in two cases, has been proved not to occur. These primarily allopatric forms are considered to be double invasions in view of their habitat preferences and of the development of highly distinctive external color differences.

The remaining seven cases are primarily sympatric and may be classified as follows:

(a) Partial range overlap with possible development of genetic and ecological differences; No. 7, *Gracula* species, and No. 8, *Zosterops* species.

(b) Range overlap with the possibility of pre-adaptation as suggested by Lack, bearing in mind that the populations may be in flux at the present; No. 5, *Megalaima* species.[2]

(c) Range overlap with obvious structural difference and a possible threshold of habitat tolerance; No. 4, *Centropus* species.

(d) Range overlap with insufficient explanation for the phenomenon of sympatric, closely related species being able to maintain themselves; No. 6, *Turdoides* species, and No. 3, *Dicaeum* species.

[2] Simpson (1944, p. 188) notes that there is probably some definite survival value involved in such population change.

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THE ROLE OF SEXUAL SELECTION AS AN ISOLATING MECHANISM IN THREE SPECIES OF POECILIID FISHES

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The role of sexual isolating mechanisms in maintaining the integrity of ecologically coincident yet specifically distinct populations of sympatric species does not seem to have been very fully investigated. In part, this may be due to the actual rarity of such complete ecological coincidence among species mixtures under natural conditions. It is well known that, among a very considerable proportion of sympatric terrestrial species, ecological differentiation, if only in response to minor features of the common environment, is sufficiently marked so that its importance as an isolating mechanism in speciation cannot be neglected. In part, the paucity of observations of this kind is undoubtedly due to the relatively small number of species mixtures of terrestrial organisms which are sufficiently well understood to make possible any certain conclusion as to the presence or absence of such ecological isolating mechanisms, or any estimate of their relative importance.

Observations upon mixtures of sympatric species the members of which were known to be essentially identical in food habits and environmental preferences would obviously be of great value in a study of the role of physiological and sexual isolating mechanisms in the absence of ecological factors. On the whole, populations of aquatic organisms seem to present more promising material for investigations of this sort than do terrestrial ones. Such truly mixed populations are perhaps most evident among freshwater organisms which inhabit streams and restricted lake environments. It seems likely, for instance, that certain members of the so-called "species swarms" of Cichlidae found in some African lakes, such as those studied by Bertram, Borley, and Trewavas (1942) and others, may properly fall within this category. In other cases, although the ecological coincidence is less perfect, there is still a large and important environmental area in which intimate species mixtures occur without any loss of distinctness on the part of either population. The geographical overlap of the viviparous Poeciliid fishes *Xiphophorus hellerii* and *Platypoecilus maculatus* in Mexican streams is well known and has been extensively studied by Gordon and his coworkers (1947).

The present report is concerned with a single aspect of a study now in progress of the ecological relations within a mixture of three sympatric species of Poeciliid fishes which show an extraordinary degree of habitat coincidence in certain of the fresh waters of Trinidad. These three species are *Lebistes reticulatus* Peters, *Micropoecilia parae* Eigenmann, and *Poecilia vivipara* Bloch and Schneider. All three are closely related taxonomically, being included by Hubbs (1926) in a single tribe, the Poeciliini of the subfamily Poeciliinae. Mixed schools of these three species of fish are found in many Trinidad waters, and they exhibit almost identical feeding habits and prefer closely similar stream environments. Such populations appear to offer unusually good opportunities for a study of the operation of sexual and physiological isolating mechanisms in speciation quite apart from the influence of ecological isolation.

THE EXPERIMENTAL MATERIAL

Poecilia vivipara, Micropoecilia parae, and *Lebistes reticulatus* are all relatively

small, largely surface-feeding viviparous top-minnows native to parts of the West Indies and northeastern South America. In Trinidad, the two first-named species are normally fish of quiet coastal streams and brackish lagoons, being especially abundant in swamps and the irrigation ditches of cocoanut plantations. *Lebistes reticulatus* occupies a wider range of habitat. It is common in relatively swift upland streams, but penetrates throughout their courses and coexists in great numbers with the other two species in lower waters. Evidence is accumulating to indicate that the populations of lagoons and lower river courses may represent a physiologically somewhat distinct race from those in swifter and fresher water, but this is by no means certain.

The food habits of the three species are closely similar. All are essentially omnivorous, picking insects and other food from the water surface and foraging at the bottom for algae, insects, and crustacea. *Lebistes* and *Micropoecilia* characteristically swim at the surface, often in intimately mixed schools. *Poecilia* sometimes appears with them, especially younger specimens, but mature individuals tend to remain at lower levels, as is true to a degree of larger females of the other two species. Since the waters in which the studies are being conducted are only about eight to twelve inches in depth, and since the smaller specimens of all three species make constant foraging trips from the surface to the bottom and back, even this habitat preference is probably of little significance.

Reproductive isolation between the three species appears to be essentially complete in nature. No intergrades have so far been found in any of the mixed populations studied. Hybrids between *Poecilia vivipara* and *Lebistes reticulatus* have been obtained in the laboratory. Phenotypically they resemble *P. vivipara* and are relatively large, well developed, and extremely hardy, but it is probable that they are sterile. It is clear, therefore, that physiological isolating mechanisms are of importance in maintaining the species structure of the population. These may involve such physical factors as differences in gonopodial structure between the species (which are considerable), factors of partial sterility involving sperm competition, or differential viability of hybrid and non-hybrid embryos. The question is being investigated further.

The role of sexual selection as an isolating mechanism is suggested by several conspicuous features in the biology of all three species. In all of them, sexual dimorphism is most pronounced, and includes important features of structure, coloration, and behavior. In *Micropoecilia* and *Lebistes* the mature male averages somewhat less than half the size of the fully grown female. In all three species, the mature male is highly colored and shows some secondary modification of fin morphology in addition to the specialized development of the gonopodium characteristic of all Poeciliid fishes. In *Poecilia* this modification of color and fins is relatively slight. At maturity an intense salmon-red coloration replaces the normal gray of the female and immature forms, but the basic reticulate melanin pattern remains unchanged. In *Micropoecilia* the mature male takes on a conspicuous coloration which is very different from that of the female and involves elaborate patterning of the dorsal and caudal fins with areas of melanin and carotinoid pigments and some characteristic coloration of the body. In *Lebistes* the mature male shows the great variety of highly polymorphic patterns of fin and body coloration which have made the guppy a favorite aquarium fish, as distinct from the coloration of the adult female as is the case with *Micropoecilia parae*.

The mature males of all three species thus differ strikingly in appearance both from the females of their own species and from each other. They are even more distinctive with respect to their courtship patterns. Elaborate and characteristic courtship patterns dominate the activities of the males and are a usual, though not

an invariable, prelude to mating. A description of these patterns would be unduly lengthy here. Suffice it to say that they are an unmistakable and, in their total complex, an invariantly distinguishing species characteristic.

In contrast to the males, the females of *P. vivipara, M. parae,* and *L. reticulatus* resemble one another to a marked degree, and this further emphasizes the interest attaching to an investigation of the role of sexual selection in isolation. The females of *Micropoecilia* and *Lebistes* are closely similar in size, conformation, coloration, and behavior. Both are of an inconspicuous gray color with fins of the generalized type common to the tribe, clear and without obvious patterning, save that some females of *M. parae* in Trinidad carry a small black spot near the upper margin of the base of the caudal fin. The females of *Lebistes* carry no pattern of body coloration save for the characteristic reticulation. The females of *Micropoecilia* show a somewhat less conspicuous reticulation and are of a slightly more golden color, with a few irregular black dots caused by local aggregations of micromelanophores. There is also a small but more or less conspicuous black lateral spot, located near the distal margin of the pectoral fin when at rest against the body and surrounded by a few gold scales. This spot tends to disappear in many old specimens. The fully mature female of *P. vivipara* averages somewhat larger in size than those of the other two species. It is also of a plain gray coloration with less evident reticulation, but with a black lateral spot, surrounded with golden scales as in the case of *M. parae* and located in a similar relative position. The fins are clear and with a more or less distinctive patterning of minute black spots. The dorsal fin is located somewhat more anteriorly than in *Micropoecilia* and the caudal fin is more sharply angulated.

In mating pattern, as in appearance, the females of the three species show no such distinctive differences as do the males. In all three cases, the female is a relatively passive agent in the mating process, responding little in any obvious way to the courtship patterns of the male. The females of *P. vivipara* and *M. parae* respond to actual gonopodial contact of the male to the extent of halting momentarily in swimming and rotating the body slightly toward the side from which the male has approached, thus facilitating such contact. This behavior pattern is common to the members of several related genera of Poeciliine fishes, such as *Mollienisia* and *Limia.* In *Lebistes,* on the other hand, the female remains throughout an apparently entirely passive agent in the whole act of fertilization. There is normally no marked halting in swimming, and no evidence of cooperation in any active way, except possibly in the case of females which have been reared in isolation in the laboratory.

The process of fertilization in *M. parae, P. vivipara,* and *L. reticulatus* is internal, as in all the Poeciliidae. Encapsulated spermatophores are probably transferred along the male gonopodium to the genital pore of the female in one or more contacts. The contact may be a relatively lengthy one, as typically in the case of *P. vivipara, M. parae, Mollienisia* and *Limia,* and notably in the cases of the Xiphophorine fishes studied by Clark, Aronson and Gordon (1948). It may, on the other hand, be swift and of momentary duration, as is commonly if not always true in *Lebistes.* This difference of mating procedure between *L. reticulatus* on the one hand and *M. parae* and *P. vivipara* on the other may be of importance to the present investigation, and will be referred to further.

Experimental Objectives and Procedure

The pronounced sexual dimorphism of coloration, form, and behavior in the males of these three species on the one hand and the conservatism and similarity of the females on the other suggests *a priori* that the selection of appropriate mates in intimately mixed populations may be largely a matter of female discrimination of and

TABLE 1. *Gonopodial contacts of fourteen males of* Lebistes reticulatus *with any of three available females immediately and after one week*

Experiment I. Four males, from Maracas River, Trinidad

	Immediately	After one week
Contacts with *Lebistes* female	56	98
Contacts with *Micropoecilia* female	34	2
Contacts with *Poecilia* female	10	0
	100	100

Experiment II. Five males, from Santa Cruz River, Trinidad

Contacts with *Lebistes* female	16		93
Contacts with *Micropoecilia* female	79	(1–100)	7
Contacts with *Poecilia* female	5		0
	100		100
	39		Not made
	59	(101–200)	
	2		
	100		

Experiment III. Five males, from St. Joseph River, Trinidad

Contacts with *Lebistes* female	28	Not made
Contacts with *Micropoecilia* female	65	(♀ *Micropoecilia* died)
Contacts with *Poecilia* female	7	

Totals:

	Initial exposure	After one week
Contact with *Lebistes* female	139 (34.7%)	191 (95.5%)
Contact with *Micropoecilia* female	237 (59.3%)	9 (4.5%)
Contact with *Poecilia* female	24 (6.0%)	0 (0.0%)

The same three females, from wild stock, were used throughout these experiments. They were selected as nearly as possible of equivalent size. Their respective measurements were:

	Lebistes	*Micropoecilia*	*Poecilia*
Weight (mg.)	402	531	612
Length (snout to base of caudal fin, mm.)	26.0	28.0	28.5
Greatest depth (mm.)	7.0	8.0	8.5

The difference in percentage of incorrect and correct choices between the first contacts and those after one week of exposure is statistically significant.

reaction to the highly distinctive stimuli of color, form, and behavior offered by the males of the proper species, and rejection of the inappropriate stimuli involved in the advances of other males. If this were true, the situation would be closely similar to that so well known and relatively so well understood among many birds. In such an event, the evolution of specialized patterns among the males could be considered as a readily understandable corollary of sexual selection in the conventional Darwinian sense, and the role of sexual selection as an isolating mechanism in this sympatric species population would be relatively straightforward. The experiments reported were designed, therefore, to test the question of whether the reaction of females of the three species to the stimuli presented by the males was specific, and of importance in assuring that only the appropriate matings should occur, as has been well demonstrated by Tinbergen and Van Iersel (1947) for the

case of the stickleback. The results have been unexpected and surprising and are currently presented with no attempt at a full explanation.

The experiments were simple in design and execution. An aquarium of fifteen gallons capacity was arranged to simulate as closely as possible a section of the lagoon environment. This arrangement was made with considerable care since it was deemed important to maintain the ecological situation as nearly intact as possible. Into this tank were introduced simultaneously three females, one of each of the three species concerned, and several males of one. The females selected were all already pregnant (the normal condition in the wild state) and wherever possible were taken directly from mass cultures of their own species. The males used were all actually wild fish taken from Trinidad waters or were first-generation descendants of such individuals. They were all taken directly from mass cultures of their own species immediately before the experiments were begun.

The males were introduced to the tank containing the three females and observations were begun within an hour. The behavior of the males was closely noted, and all gonopodial contacts with females of each species were recorded. When 100 or 200 such recordings were made, the observations were discontinued for a period of six days and the fish left undisturbed *in situ*. On the sixth day another set of 100 observations of gonopodial contacts was made. The males were then removed, the females being left in place alone for twenty-four hours. A new group of males was then introduced and the observations were repeated.

Owing to the much greater sexual activity of *Lebistes* males than of males of the other two species it proved experimentally most convenient to work with them. All records presented in this series, therefore, refer to the behavior of *Lebistes* males in the presence of females of the other species.

It is well known that males of *Lebistes*, when exposed to several females of their own species, tend to pay most attention to the largest individuals, and the size differential among them need not be great. Especial care was used, therefore, to select females of closely similar size. Rec-

TABLE 2. *Gonopodial contacts of single male of* Lebistes reticulatus *with any of six females of three species over a period of nineteen days*

Single male, from the Arima River, Trinidad
Two females each of *Lebistes reticulatus* (Arima River), *Micropoecilia parae*, and *Poecilia vivipara*

Date	Contacts with *Lebistes*	Contacts with *Micropoecilia*	Contacts with *Poecilia*
10/22/47	15 (30.0%)	34 (68.0%)	One approach, no contacts (2.0%)
10/23/47	34 (68.0%)	16 (32.0%)	0 (0.0%)
10/27/47	58 (100.0%)	0 (0.0%)	0 (0.0%)
10/28/47	98 (98.0%)	1 (1.0%)	1 (1.0%)
10/31/47	68 (98.6%)	0 (0.0%)	1 (1.4%)
11/2/47	93 (98.9%) (Male *M. parae* introduced)	0 (0.0%)	1 (1.1%)
11/4/47	53 (98.1%) (One female of *P. vivipara* died. Replacement introduced. This created no excitement.)	1 (1.9%)	0 (0.0%)
11/8/47	86 (100.0%)	0 (0.0%)	0 (0.0%)
11/10/47	38 (97.4%)	1 (2.6%)	0 (0.0%)

Errors were high on the first two days, as in the initial exposures recorded in table I. By the third day, discrimination had become remarkably good, and remained so to the end.

ords are given of the weights of each female, the length from snout to base of caudal fin, and the greatest body depth. Since the same females were used throughout, their states of pregnancy varied with the experiment. Parturition was observed in none of them during the work. The males used were from stock taken from three distinct Trinidad locations. The female *Lebistes* were taken from one of these. Fourteen males were involved, and observations were made of 600 gonopodial contacts. The data are summarized in table 1.

As a check upon these experiments, a more detailed and complete series of observations was made involving a single male and two females of each of the three species, so matched for size that a larger and a smaller individual of each species was present. As in the previous situation, records of 600 gonopodial contacts were made, and courting behavior was carefully noted. Observations were made for a period of approximately ten hours, distributed over a period of twenty days. The data are summarized in table 2.

Discussion

The experiments described included observations on the behavior of fifteen wild *Lebistes* males from four environments in Trinidad when exposed to wild females of their own and the other two sympatric species. In all, 1200 gonopodial contacts were recorded. In two experiments the *Lebistes* females were taken from the same actual body of water as the males. In two cases they were from adjacent and similar, but not identical, locations. This made no observable difference.

The results are on the whole uniform in character. In every case the males showed an initial preponderant choice of the females of *Micropoecilia parae* with which to make gonopodial contact. In every case this initial error of choice was striking. It was clearly aided by the behavior of the females of *parae,* which reacted to the *Lebistes* males in exactly the fashion characteristic of their reaction to males of their own species, halting in swimming and rotating the body, thus cooperating in the formation of contact—a procedure never seen in *Lebistes* females from mass culture as already indicated. A number of erroneous contacts were also made with *Poecilia vivipara.* These were in all cases less numerous, although the reaction of the *vivipara* female was likewise typical of its reaction to males of its own species, and therefore slightly positive. Throughout the experiments the reactions of the females of *parae* and *vivipara* to males of *Lebistes* differed in no detectable way from those normal to their own species. No evidence of female discrimination has been found so far.

After a relatively short time, the errors in gonopodial contact were sharply reduced, as will be seen, and in every case observed finally reached a very low level. In all the observations, there was every indication that this rectification followed from a learning process on the part of the *male alone.* Females of the other species continued to react positively to the relatively few gonopodial contacts which were achieved. After prolonged exposure, males regularly continued to approach the females of *Micropoecilia parae* as they had earlier, poised or executed typical courtship patterns, but then turned away sharply without contact.

Three impressions are very strongly given by these observations. First, discrimination of the correct females by wild males of *Lebistes* in mixed populations of the three sympatric species can be carried out with a high degree of accuracy if the populations have been in equilibrium for a period of twenty days or more. Sexual selection, therefore, favors the transfer of more gametes to the correct than to the incorrect females. This is in accord with the general principle of the "conservation of gametes" originally stated by Dobzhansky and recently further elucidated by Mayr (1948). An estimation of the importance of sexual selection as an isolating mechanism in this situation must await a

more complete estimate of the extent of physiological isolation which is involved.

The second and more striking impression, which has been consistent under varying conditions, is that this discrimination is made on the part of the male alone, the female being an essentially passive agent in the process. This is the reverse of what might be expected in view of the similarity of the females of the three species and the marked differentiation of the males, but is consistent with the hypothesis advanced by Noble and Curtis (1935) that the selection basis of male coloration in *Lebistes* is that of warning between males rather than stimulation of females.

Third, and perhaps most striking, the evidence seems very good that the discrimination of *Lebistes* males which have been kept for long periods in mass cultures of their own species alone is at first exceedingly imperfect, and that a high order of perfection is achieved gradually, the reaction being apparently a learned one.

There are three questions which are important in analyzing these conclusions and in applying them to a study of natural populations of these sympatric species. First, what is the meaning of the "gonopodial contact" in genetic terms? Does each gonopodial contact represent an actual transfer of sperm, or are the great majority of these contacts without specific genetic meaning? Second, cannot the initially large percentage of errors of the *Lebistes* males be explained merely as a high and therefore uncritical threshold which was gradually lowered by "saturation" of contacts until only stimuli from the correct females was sufficient to evoke the contact reaction? If this were true, there would be no indication of any learned reaction, but only of a lowered generalized reaction threshold. Third, is it really clear that reactions on the part of the female, too small to be noticed by the observer, were not actually responsible in part for the discrimination observed? Is it clear, in other words, that there is not in fact here a series of "reaction chains" between male and female, differing from the similar situation recorded for many other organisms only in that it is more difficult to detect? These questions require some further discussion.

1. *The Genetic Meaning of the "Gonopodial Contact" in* Lebistes

Clark, Aronson and Gordon (1948) have made rather extensive observations on the process of fertilization in *Xiphophorus hellerii* and *Platypoecilus maculatus,* among themselves, in crosses, and among the F_1 hybrids. They have reported the existence of two rather distinct types of gonopodial contact, the first, which is more frequent, being momentary and somewhat of the *Lebistes* type, the second less frequent and more prolonged. It has been shown by the method of smears that the transfer of sperm takes place only in the second type of contact.

It is necessary to know, therefore, that in *Lebistes* the observed type of contact results, at least in many cases, in the actual transfer of sperm. There is some evidence that this is true. In many thousands of observations of *Lebistes,* no type of gonopodial contact other than that observed in these experiments has been distinguished, and no observations of other types of contact have been recorded, so far as the authors are aware. The question, however, is being further investigated experimentally.

Thus evidence seems indicative that sperm transfer is actually effected from *Lebistes* males to *Lebistes* females by gonopodial contacts of the type recorded. It does not, of course, indicate the percentage of cases in which such transfer is effected. Experiments are currently in progress to determine this by exposing virgin females to single and to counted multiple contacts and thereafter sectioning them to determine the percentage of ova that are fertile in each case. The results of this work are not yet available. The evidence also does not indicate that sperm transfer from *Lebistes* males occurs successfully in the case of a similar percentage of er-

roneous contacts, although the fact that it can be successfully accomplished in the case of *P. vivipara* is proved by the laboratory hybrids which have been produced. This question is an important one, but belongs in the study of physiological isolating mechanisms now in progress.

2. *Erroneous Contacts and Male Threshold versus "Learned" Reactions*

The processes of sex recognition and courting in *Lebistes* have been extensively studied by Breder and Coates (1935) and by Noble and Curtis (1935). The former authors observed that sexually active males will attempt to fertilize a variety of objects more or less indiscriminately. The specimens with which they worked reacted positively to anaesthetized females of their own species and to specimens of *Cyprinodon variegatus, Fundulus heteroclitus,* and *Barbus conchonius,* as well as to the shadows of living fish projected on the sides of the aquarium. These observations would seem to indicate that the "threshold" in *Lebistes* males is extremely low, and that, in the present experiments, the increasing perfection of discrimination did in fact represent a progressive raising of that threshold through "saturation." It is to be noticed, however, that the *Lebistes* males used by Breder and Coates had been isolated from all females for one week before experiments were begun. In contrast, males used in the present experiments were taken directly from cultures in which many female *Lebistes* were present, and should therefore have been as "saturated" at the beginning of the experiment as at the end. Noble and Curtis, on the contrary, used males which had had free and continuous access to females of their own species, and reported greater success and higher discrimination on the part of old and "experienced" males, while young males reared alone attempted at first to mate with males, but gradually came to correctly discriminate males from females—results which tend to substantiate the hypothesis of a "learned" reaction in the present case.

3. *Role of the Lebistes Female in Determining Correct Contacts*

It is extremely important theoretically to determine whether mate selection in *Lebistes* is in fact a function of male discrimination only, or whether a "chain" of reactions exists between male and female, resulting in the accumulation of stimuli which eventually culminate in fertilization, as has been demonstrated for many other organisms. As already mentioned, no visual evidence of this situation has been found, although it has been very carefully looked for.

To test the matter further, a rather extensive series of observations are in progress which will be reported elsewhere. Though not yet completed, enough evidence has accumulated to be significant. Experiments have been set up identical to those reported here, except that the *Lebistes* have been given a choice, not of females of three species, but of females of three genetically homogeneous strains of *Lebistes* differing among themselves in only a single autosomal gene. In every case so far studied, wild type males have been used, taken from mass cultures of genetically homogeneous wild-type strains, and the choice given has been between wild-type females of the same strain and two classes of females of the same strain but carrying a recessive allele for xanthic body coloration.[1] These females are otherwise completely normal and are fully interfertile with the wild strain. In these experiments also, initial "errors" were high, but after several days of association, the percentage of discrimination of wild-type females by these wild-type males was as good as at the close of the experiments here reported. It seems extremely unlikely that in all these cases the single autosomal gene difference of the mutant fe-

[1] These body-color alleles to wild-type are "golden" and "blond" described by Goodrich (1944), Winge (1947), Haskins and Druzba (1938), and Haskins and Haskins (1948).

males would markedly influence their sexual behavior so as to break the chain of mutual stimulation if it existed. Discrimination on the part of the male alone seems much the simpler explanation.

The evolutionary significance of this situation requires further analysis, but it is suggestive that the function of male sex coloration, at least in *Lebistes,* is wholly a repellant one between males, and plays little part in sexual isolation, while male discrimination, on the other hand, is important in this connection.

Summary and Conclusions

Preliminary studies are described designed to explore the mechanism of sexual selection and its role as an isolating mechanism among populations of three sympatric species of Poeciliid fishes which normally coexist in the coastal waters of Trinidad and which exhibit an extremely low degree of ecological isolation. The studies have involved the reactions of fifteen males of *Lebistes reticulatus,* taken from four separated locations in Trinidad, to wild females of *Lebistes,* of *Micropoecilia parae,* and of *Poecilia vivipara.* The study is still in progress, but three tentative conclusions seem justified on the basis of the data reported and of certain auxiliary experiments which are described. These conclusions are:

1. Measuring the reaction of the male *Lebistes* to females of its own and the other species by the relative frequency of gonopodial contacts, a rather good discrimination of *Lebistes* for *Lebistes* exists in mixed populations which are at equilibrium.

2. This discrimination is based essentially upon the behavior of the male, despite the fact that in all three species pronounced sexual dimorphism exists on the part of the male in form, coloration, and courtship patterns, while the females have remained markedly conservative on all three scores. It has not been possible to obtain any evidence of a "chain" of stimulation reactions between male and female, and some fairly convincing evidence has been obtained against it.

3. Discrimination among males which have been kept with females only of their own species is at first very poor, but improves rapidly in a matter of days until a high efficiency is attained. Females of alien species, on the other hand, continue to tolerate erroneous contacts with the same degree of readiness at the end as at the beginning of the experiments, showing no detectable change of behavior. The change of behavior on the part of the males gives some evidence of being a "learned" reaction.

Work is in progress to investigate this situation by other methods, as well as to determine more completely the degree of physiological isolation between these species, which appears to be considerable.

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INTERSPECIFIC MATINGS BETWEEN *COLIAS EURYTHEME* AND *COLIAS PHILODICE* IN WILD POPULATIONS

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The act of copulation between the sexes of two different species has not often been actually observed in wild populations. More often hybridization has been assumed from the presence of intermediates or hybrids in the respective populations. Owing to the rarity of data showing the actual rather than the assumed hybridization, the following data may be of interest.

The two butterflies *Colias eurytheme* and *Colias philodice* apparently hybridize in most areas where their ranges are in contact or overlap. This hybridization however does not result in the expected elimination of both species in favor of an intermediate type. Rather, the two species maintain themselves year after year in the same areas despite constant exchange of genes from one species to the other.

The result of the hybridization is the production of F_1 hybrids between the two parental species which are intermediate in their phenotypical characteristics. But the hybridization does not stop there. Backcross progeny and F_2 hybrids are also produced, thus leading to a population having individuals ranging from the one parental form to the other with no sharp line of demarkation. It has been found that these intermediate types rarely exceed 10 per cent of the entire population numbers (Hovanitz, 1943; Gerould, 1946).

Interspecific crosses in the laboratory have been observed by Gerould (1943) and Hovanitz (1944) and in wild populations by Hovanitz (1943). However, no quantitative data have ever been published which would indicate the relative proportions of these hybrid crosses as compared with the intraspecific matings.

The following data were obtained on October 26, 1947 in an alfalfa field near Celina, Ohio (for map see Hovanitz, 1948). The characteristics of this field were those favoring the presence of a considerable number of copulating pairs. Males were swarming over the field but females were relatively scarce. Both males and females were in the emerging cycle. Copulating pairs were collected as given in table 1. Grades of orange pigment from 8 to 10 are considered to be *Colias eurytheme* and grade 1 to be *Colias philodice;* grades 2 to 7 are considered to be hybrid products.

TABLE 1. *Copulating pairs of* Colias eurytheme *and* Colias philodice *collected in an alfalfa field near Celina, Ohio*

Orange grades 8–10 are pure orange *C. eurytheme* and orange grade 1 is pure yellow *C. philodice*. As both species have a white female dimorphic form, the latter have been further classified as to species.

Male		Female	Actual number of pairs
eurytheme × *eurytheme*			*16*
grade 10	×	grade 10	1
grade 10	×	grade 9	3
grade 9	×	grade 10	1
grade 8	×	grade 10	2
grade 10	×	white *eurytheme*	5
grade 9	×	white *eurytheme*	1
grade 8	×	white *eurytheme*	3
eurytheme × *philodice*			*1*
grade 10	×	grade 1	1
eurytheme × intermediates			*1*
grade 10	×	grade 6	1
intermediates × *eurytheme*			*3*
grade 7	×	grade 9	1
grade 2	×	grade 9	1
grade 6	×	white *eurytheme*	1
total			*21*

Of the twenty-one pairs collected in this field, sixteen were of the cross *C. eurytheme* × *C. eurytheme*, one was of the cross *C. eurytheme* × *C. philodice* and

four were of various combinations of intermediates with *C. eurytheme.*

The intermediates could not be designated as certainly F_1, F_2 or backcross progeny of the two species but have merely been graded. In laboratory crosses, the F_1 would be either grade 5 or 6; the F_2 would be from grade 1 to 10 and would include many which are similar to the F_1; the backcross progeny would include both parental types as well as intermediates between them and would thus include types similar to the F_1 and the F_2. Intermediates which were involved in the matings in this field are of grades 2, 6 and 7. Genetically-possible grades of intermediates higher than grade 7 are not distinguishable from the parental *C. eurytheme* owing to the natural range of variability present in that species.

Since both *Colias eurytheme* and *Colias philodice* have dimorphic females in which the ground color of the wings is white, the grade of orange naturally could not be indicated. Determination as to species or intermediates was made however by means of pattern differences of the two species shown by Gerould (1946).

It is of interest to determine whether the three classes, *C. eurytheme, C. philodice* and intermediates, were present in copulating pairs in the same frequency as in the free flying individuals. Composition of the entire population was determined and is shown in table 2. A total of 206 males and 130 females was obtained. Since selection was made for females, the discrepancy in the sex ratio was probably much larger than indicated rather than smaller.

In both the males and females there is a nearly complete range of intermediates from grades 1 to 10. However, the concentration of intermediates is on the *eurytheme* side. The frequency of the three classes is quite different, being 11.9% *C. philodice,* 9.21% intermediates and 78.87% *C. eurytheme.* The distribution into classes is very similar for the two sexes.

The distribution of the species and intermediates in the population as compared with the same in copulation at this locality is shown in table 3. There is a difference indicated for both the males and the females. A higher frequency of *C. eurytheme* is shown in the copulating individuals than in the population as a whole. The frequency of intermediates among the copulating individuals does not differ from

TABLE 2. *Composition of the population at Celina, Ohio with respect to* Colias eurytheme, Colias philodice *and intermediates between them*

A. Actual numbers

	Grades of orange										Species of white female			Total
	philodice	intermediates						*eurytheme*			*philodice*	intermediates	*eurytheme*	
Grades	1	2	3	4	5	6	7	8	9	10				
Males	24	1	1		3	6	10	33	47	81				206
Females	13			1	1	2	3	7	20	34	3	3	43	130

B. Percentage

	Colias philodice	intermediates	*Colias eurytheme*
Males	11.65	10.19	78.16
Females (normal)	10.00	5.39	46.92
Females (white)	2.31	2.31	33.08
Females (total)	12.31	7.69	80.00
Males and females	11.90	9.21	78.87

TABLE 3. *The distribution of species and intermediates in the population as compared with the distribution of the same in copulation at Celina, Ohio*

	eurytheme		intermediates		*philodice*		Total
	%	N	%	N	%	N	N
Population, males	78.16	161	10.19	21	11.65	24	206
Copulation, males	85.71	18	14.29	3	0.00	0	21
Population, females	80.00	61	7.70	7	12.31	13	130
Copulation, females	90.48	19	4.76	1	4.76	1	21
Population, total	78.87	222	9.21	28	11.90	37	336
Copulation, total	88.10	37	9.52	4	2.38	1	42

(Significance of difference between population total and copulation total, $P < .02$ that a difference as great as that shown would occur due to chance alone.)

that of the population as a whole. *Colias philodice* shows the antithesis of *C. eurytheme,* having a much higher frequency in the population as a whole than in the copulating individuals.

The significance of the difference was tested by the chi-square method, assuming that the proportion of each class in the population as a whole to be the frequency expected of these classes among the copulating group. For three degrees of freedom, a probability of less than .02 was indicated that the difference would be as large due to chance alone. It seems likely, therefore, that the lower frequency of *eurytheme* or the higher frequency of *philodice* in the population as a whole is due to some factor other than chance alone.

A further test has been made on the frequencies of the actual pairs found in the field. Six different combinations of the three classes are possible as shown in table 4. These six different kinds of pairs should be present in a definite proportion provided that mating between all the individuals was at random. The expected proportions may be determined by expansion of the trinomial $(p + q + r)^2$ where p = the frequency of *C. eurytheme,* q = the frequency of *C. philodice,* and r = the frequency of the intermediates. This expansion is $p^2 + 2pq + 2pr + q^2 + 2qr + r^2$. The frequency of the three classes is given in table 3.

The actual and the expected frequencies of the six combinations that could be expected in the population are shown in table 4. It is seen that even with a relatively small number of individuals, the actual frequency of the combinations is very close to the expected. Only three of the six combinations appeared. The other three were not expected to appear in a sample as small as twenty-one pairs. The results were tested by chi-square and agreement is found to be quite close, $P > 0.5$, that a deviation greater than that observed might occur due to chance alone.

These data indicate that there is little selection among the individuals in the *Colias eurytheme* and *C. philodice* populations at Celina, Ohio, for mates of the same species, the other species or the intermediates. Mating appears to be at random so far as this small sample is concerned.

TABLE 4. *The frequencies of pairs of the three classes,* C. eurytheme, *intermediates and* C. philodice

			actual	expected
Colias eurytheme	× *C. eurytheme*	p^2	16	13.07
Colias philodice	× *C. philodice*	q^2	0	0.30
Intermediate	× intermediate	r^2	0	0.18
C. eurytheme	× *C. philodice*	$2pq$	1	3.94
C. eurytheme	× intermediate	$2pr$	4	3.04
C. philodice	× intermediate	$2qr$	0	0.46

(Significance of the difference, $P > .5$ with five degrees of freedom that the variations are due to chance alone.)

The fact that a higher frequency of *Colias eurytheme* (or a lower frequency of *Colias philodice*) is present in the copulating individuals than in the population as a whole is probably due to the nature of the field in which the sampling was made. In this area *Colias eurytheme* prefers alfalfa fields to clover fields and *Colias philodice* prefers clover to alfalfa (Hovanitz, 1948). Therefore, it might be expected that freshly emerging individuals of *C. eurytheme* rather than *C. philodice* would be common in the alfalfa field. Those examples of *C. philodice* found in the alfalfa field would more likely have come from a nearby clover field. Mating in the females of *Colias* occurs generally only once and that very soon after emergence from the pupa. If many males are present in a field where females are emerging, the females will often be found in copulation before their wings are yet dry and before they are able to fly. For this reason therefore fewer *C. philodice* than *C. eurytheme* would be expected among the copulating population in an alfalfa field such as this one.

Summary

Analysis was made of the Colias butterflies in an alfalfa field in Ohio where *Colias eurytheme* and *Colias philodice* were hybridizing. A number of copulating pairs was secured and the frequency of the types in the population as a whole as compared with those in copulation was determined. It was found that the frequency of *Colias eurytheme* was higher and that of *Colias philodice* was lower in the copulating individuals than in the population as a whole. This fact can probably be related to the greater emergence of *eurytheme* in the alfalfa field than of *philodice*. Mating takes place soon after emergence from the pupa. It was also found that the actual frequency of the mating pairs in the field was very similar to the proportions expected on the basis of their abundance in the field. Mating appears to be at random.

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ANALYSIS OF DATA ON SEXUAL ISOLATION

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Following the recognition by Dobzhansky of the importance of sexual isolation in speciation, especially in the genus *Drosophila,* a number of experiments have been made on mating discrimination between races of various *Drosophila* species: *willistoni* (Dobzhansky and Mayr, 1944), *sturtevanti* (Dobzhansky, 1944) and *prosaltans* (Dobzhansky and Streisinger, 1944) and between the species *pseudoobscura* and *persimilis* and their hybrid (Mayr, 1946a). Tan (1946) has made a similar study of the effects of mutants in *pseudoobscura.*

A brief account of the technique is necessary here. Equal numbers of two strains of females are enclosed with males of one of these strains. After a lapse of time sufficient to produce about 50% insemination the distribution of inseminated females between the two strains is observed. The percentage of intra-strain matings minus the percentage of inter-strain matings, divided by their sum, is the isolation index. If all matings are intra-strain the index is 1. If all matings are inter-strain the index is -1. If both strains are equally inseminated the index is zero.

Since one strain of males is enclosed with two strains of females it is tempting to assume that the results are determined by discrimination on the part of the males. Both the direct (Mayr, 1946b) and indirect (Bateman, 1948) evidence is quite contrary to this assumption. Virtually conclusive was Streisinger's experiment (1948). Etherization of females, by inhibiting any discrimination on their part, enabled interspecific matings which were otherwise impossible to take place freely. It is justifiable to suppose that the determining factor in "choice" matings is the degree to which the two strains of female repel the same males.

It is unfortunate, in view of the role of the females in determining sexual isolation, that in experiments of the "choice" type it is always the males rather than the females which have been offered the choice. The technical difficulties confronting the female "choice" matings are great. If they could be overcome, however, they might be more sensitive than the matings usually used.

The repulsion exercised by the females will be the result of two sets of factors. The first, which is strictly concerned with sexual isolation, will depend on the ability of females to perceive whether the male is of their own or another strain and the degree to which they are capable of repelling males which they "recognize" as foreign. The second is concerned with the non-specific mating propensity of the females (what might be called their "heat"). Mayr (1946 a and b) has proposed that the more active the female the more likely she is to be courted. This does seem to apply when one compares females of the species *D. pseudoobscura* and *D. persimilis.* On the other hand, if a female is trying to avoid mating, the more active she is the more successful she will be. The situation is probably a complex one. The relative mating propensity of females of different strains introduces a complication to the study of sexual isolation which it may mask or exaggerate, sometimes even producing negative isolation indices, which are inexplicable by the theory of sexual isolation.

It is possible, however, to separate the effects of sexual isolation from those of mating propensity by the use of the isolation indices from complementary matings. "Complementary matings" is here used of the pairs of matings of the types (A + B) ♀♀ × A ♂♂ and (A + B)

♀♀ × B ♂♂. Half the sum of the complementary isolation indices is a measure of true sexual isolation. Half the difference is a measure of the relative mating propensities of females of the two strains.

It will be seen from the following analyses that the combination of complementary indices in this way rarely produces a strong negative joint isolation index. On the other hand much greater reliance can be placed on a positive joint isolation index than on the indices taken singly, since the effect of mating propensity has been removed.

In the experiments with *D. willistoni* and *D. sturtevanti* the proposed analysis is not required, for the crude data are readily interpreted. In the first species there is no sexual isolation evident and only a little variation in mating propensity. In the second species there is strong sexual isolation without any complications due to variation in mating propensity.

D. prosaltans, however, provides a good example of the value of a more precise analysis (see table I). There is a very striking gradation in mating propensity from the high values of Zopilote and Chilpancingo at one extreme to the Brazilian strains at the other. In the crude data this is sufficient to mask any sexual isolation. Using the joint index, however, we can see that there is a high degree of sexual isolation between many strains: between Guatemala and the three Brazilian strains, between Zopilote and Belem, between Chilpancingo and Iporanga, and between Belem and Bertioga. The isolation appears to be specific between particular pairs of strains. Thus Zopilote and Chilpancingo, though similar in all other respects, including place of origin, differ in their isolation from Iporanga and Belem. The apparently unpredictable nature of the sexual isolation is strong evidence that the isolation has not developed between local strains otherwise likely to interbreed, nor inversely with relationship (geographical proximity). It is explicable rather as a result of drift in small populations, correlated response to selection for local ecotypes, or both. Using the method of joint indices, *D. prosaltans* shows about as much true intraspecific sexual isolation as *D. sturtevanti.*

The method of analysis is particularly helpful in the interpretation of Mayr's re-

TABLE 1. D. prosaltans. *Isolation indices of original data*
(From Dobzhansky and Streisinger, 1944)

		♂♂ and ♀♀						
		Chil.	Zop.	Hui.	Guat.	Ipo.	Bel.	Bert.
♀♀	Chilpancingo		.00	−.47	−.27	−.31	−.47	−.58
	Zopilote	.19		−.44	−.35	−.45	−.11	−.35
	Huichihuayan	.49	.35		−.14	−.16	−.31	−.23
	Guatemala	.54	.60	.31		.22	.55	.24
	Iporanga	.75	.48	.26	.68		−.04	.05
	Belem	.54	.57	.71	.67	.03		.32
	Bertioga	.87	.57	.54	.69	.12	.19	

Joint isolation indices							Mating propensity of rows over columns					
Zop.	Hui.	Guat.	Ipo.	Bel.	Bert.		Zop.	Hui.	Gaut.	Ipo.	Bel.	Bert.
.10	.01	.14	.22	.04	.15	Chil.	.10	.48	.41	.53	.51	.73
	−.05	.13	.02	.23	.11	Zop.		.40	.48	.47	.34	.46
		.09	.05	.20	.16	Hui.			.23	.21	.51	.39
			.40	.61	.47	Guat.				.23	.06	.23
				.01	.09	Ipo.					.04	.04
					.26	Bel.						−.07

sults involving the hybrid between *D. pseudoobscura* and *D. persimilis* (table 2). Only females of the hybrid could be used in the tests because the males are sterile. The isolation indices are symbolized by the letters $a - f$.

Then the isolation index between the parent species is

$$\frac{c+d}{2} = 0.55 = s.$$

The greater mating propensity of *pseudoobscura* as compared with *persimilis* females is given by three differences:

$$\frac{(d-c)+(e-a)+(f-b)}{6} = 0.27 = m_{ps}.$$

Similarly $m_{per} = -0.27$.

The mean difference in isolation in reciprocal crosses ("cytoplasmic effect") is

$$\frac{(b-a)+(e-f)}{4} = 0.12 = c.$$

As a null hypothesis we can assume that the hybrids show no chromosomally determined discrimination, and that the mating propensity of the hybrid is mid-way between the parent species, i.e. zero. The comparison between observed indices and those calculated using only the terms s, m and c is shown in table 2. The results can be adequately explained on the assumptions made, from which we can conclude the following.

(a) The hybrid females have no chromosomally determined discrimination. This would be so if discrimination were determined by a delicate gene balance which was destroyed in the hybrid.

(b) The hybrid females have a mating propensity mid-way between the parent species. Mayr thought it was necessary to assume hybrid vigor, producing high mating propensity. The logic of this has been queried above. In any case the analysis makes such an assumption unnecessary.

(c) There is a certain maternally determined discrimination. This might involve cytoplasmic inheritance, though Tan's results (1946) do not support this explanation, for the back-cross hybrids behaved alike whichever cytoplasm they had.

One might anticipate that mutant stocks of *D. pseudoobscura* would show little sexual isolation amongst themselves. Examination of Tan's data (table 3) does, however, show a few cases of high positive joint isolation indices. All but one involve isolation between *y sn v co sh* and the rest. The six indices involving *y* (yellow body color) rank 1, 2, 4, 5, 8, and 11 among the 21 calculated indices. It has been shown even more strikingly in *D. subobscura* (Rendel, 1944) that *y* males are rejected by non-*y* females but not by *y* females. On the other hand non-*y* males inseminate *y* and non-*y* females indiscriminately. The overall effect of this one-sided action of *y* on mating behavior is the sexual isolation of *y*. It is reflected in a high joint isolation index between *y sn v co sh* and the rest and a high mating propensity for *y sn v co sh* females.

TABLE 2. D. pseudoobscura, D. persimilis *and the hybrid: isolation indices* (From Mayr 1946a)

		Males and females							
		persimilis				*pseudoobscura*			
		Symbol	Formula	Indices		Symbol	Formula	Indices	
				Observed	Calculated			Observed	Calculated
Females	*per*					*d*	$m_{ps}+s$	0.84	0.82
	per×*ps*	*a*	$m_{per}-c$	−0.32	−0.39	*e*	$m_{ps}+c$	0.42	0.39
	ps×*per*	*b*	$m_{per}+c$	−0.15	−0.15	*f*	$m_{ps}-c$	0.11	0.15
	ps	*c*	$m_{per}+s$	0.27	0.28				

TABLE 3. D. pseudoobscura *mutants. Isolation indices of original data* (From Tan, 1946)

	Males and females							
		+	*or*	*or pr*	*ast*	*w*	*BaCy*	*y* etc.
Females	+		.12	.20	.00	−.09	.00	.17
	or	−.21		−.04	− .20	−.01	−.10	.46
	or pr	.04	−.13		−. 40	.54	−.06	.30
	ast	.07	.39	.15		.15	.23	.78
	w	.10	−.03	−.10	.08		.04	.65
	BaCy	.14	.17	−.01	−1.00	−.30		.18
	y etc.	−.07	−.11	.03	− .05	−.01	.03	

Joint isolation indices							Mating propensity of rows over columns					
or	*or pr*	*ast*	*w*	*BaCy*	*y* etc.		*or*	*or pr*	*ast*	*w*	*BaCy*	*y* etc.
−.05	.12	.04	.01	.07	.05	+	−.17	−.08	.04	.10	.07	−.12
	−.09	.10	−.02	.04	.18	*or*		−.05	.30	−.01	.14	−.29
		−.13	.22	−.04	.17	*or pr*			.28	−.32	.03	−.14
			.12	−.39	.37	*ast*				−.04	−.62	−.42
				−.13	.32	*w*					−.17	−.33
					.11	*BaCy*						−.08

The other two cases of high joint isolation indices are sporadic and inexplicable in themselves. The first shows isolation between *w* and *or pr*, the second *negative* isolation between *ast* and *Ba Cy*. In the mating propensity table the only notable feature apart from the behavior of *y* is the low propensity of *ast* females. Possibly the *aristapedia* condition reduces their ability to detect courting males.

SUMMARY

On the assumption that females alone exercise mating discrimination in *Drosophila*, the effects of sexual isolation proper and differential mating propensity can be separated in experiments. A suitable method is proposed and its use is illustrated by means of examples from the published literature.

The data on *D. prosaltans* are inconsistent with a simple relationship between geographic and sexual isolation. The hybrid between *D. persimilis* and *D. pseudoobscura* behaves just as one might expect, without discrimination against either species, after allowance has been made for mating propensities.

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NOTES AND COMMENT

ESSAY-REVIEW OF RECENT WORKS ON EVOLUTIONARY THEORY BY RENSCH, ZIMMERMANN, AND SCHINDEWOLF

GEORGE GAYLORD SIMPSON

For some ten years Central Europe and the West have been separated by a highly effective intellectual isolating mechanism, only now beginning to break down. This barrier to interthinking virtually stopped the interchange of knowledge and ideas between the respective populations, within each of which the development of evolutionary theory continued independently of that within the other. The phenomenon is in some ways analogous to the results of cessation of inter-breeding, stopping the interchange of genes between populations and resulting in their independent biological evolution. Explicitly, aspects of parallelism, convergence, and divergence occur among both the intellectual and the biological results of isolation.

It is the purpose of this essay-review to examine some of these phenomena in the field of evolutionary theory and also to help to end the isolation by making more widely known some of the recent German work in this field. Such work continued with diminished and yet with considerable vigor during the period of isolation. It is not proposed here to consider all of this work, but rather to concentrate attention on three publications which seem representative of the best recent German thought on the subject, which are outstanding studies that should become known to all students of evolution, and which exemplify in their different ways evolutionary phenomena of intellectual isolation. These selected publications also represent three major fields of evolutionary study: zoology (Rensch), botany (Zimmermann), and paleontology (Schindewolf).

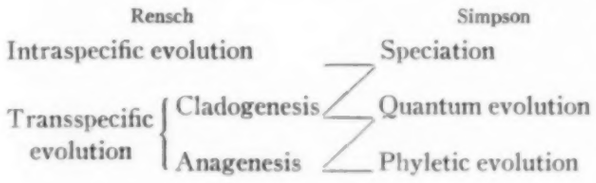
Isolation has, of course, worked both ways; western students have been isolated from German scholars as much as the reverse. It is, however, assumed that readers of EVOLUTION are by now quite familiar with the main trends in western evolutionary studies during this period. These trends have been surprisingly uniform. Although using, at times, radically different data and working in widely distinct fields, western students have in almost all cases tended toward a synthesis the core of which is the action of natural selection on genomes in populations.

Of the three German works here under review, two also arrive at essentially the same, or certainly closely congruent, conclusions. Rensch (1947) was actively participating in this trend before the war. He carried it forward during the period of isolation in remarkably close parallelism to work going on elsewhere, unknown to him. Rensch, himself, points this out in a brief appendix referring to three publications (Huxley, 1942; Mayr, 1942; Simpson, 1944) received after his book was in type. Zimmermann (1948) shows no evidence of acquaintance with these or other recent non-German publications, and indeed makes little reference to any non-German work, new or old. He departs from premises quite different from those of the modern synthesis, in which Rensch participates, and yet his views converge toward this and are in general compatible with it. As may be expected of convergence as opposed to parallelism, Zimmermann's agreement with this synthesis is, however, neither so close nor so extensive as in the case of Rensch.

The third work under review here, that of Schindewolf (1945), is in radical disagreement and exemplifies the phenomenon of divergence in intellectual evolution. Schindewolf, like Rensch and unlike Zimmermann, departed, in the main, from somewhat the same basis that has produced the synthesis and he was, indeed, a pioneer in one aspect of it (Schindewolf, 1936, an attempted synthesis of genetical and paleontological data). Divergence began, however, even in this earlier work and Schindewolf has now developed a general theory of evolution profoundly different from that of Rensch, Zimmermann, most English and American students, and many in other countries.

Rensch has long been one of the great authorities on speciation in a narrow sense, on what he calls "intraspecific evolution," and his fundamental work in this field (especially Rensch, 1929) is known to all students of evolution. In his new book, he summarizes this subject only briefly and turns his attention, rather, to "transspecific evolution," to the origin of higher categories and to the broader, more long-continued aspects of the history of life. After relatively short, but extraordinarily interesting and valuable, discussions on the lack of an over-all directional control in evolution and on rates of evolution, he divides transspecific evolution into two main aspects for which he proposes the names "cladogenesis," splitting or branching of phyletic lines, and "anagenesis," progressive change (without, or regardless of, branching). He thus pictures the whole pattern of evolution as analyzable into three main aspects, which are analogous but not identical with the three aspects

that I called major modes of evolution in my earlier study that so closely parallels Rensch's in many respects (Simpson, 1944):



Rensch does not believe (nor do I) that these different modes have categorically different causes or are basically separable evolutionary phenomena. They are simply different aspects of what is really a single, but an almost inconceivably complex, phenomenon. The phenomenon could thus be analyzed in many different ways with equal validity and there is no essential contradiction involved in the fact that I have called "speciation" aspects included by Rensch in both "intraspecific evolution" and "cladogenesis" or that "cladogenesis" and "anagenesis" both include some changes of the sort I have called "quantum evolution." Nor is the difference in terminology important as long as each author clearly defines his own usages. (And I freely recognize and share some objections to my own terms, apart from their definitions.)

In some respects, however, the concepts involved in Rensch's classification of these evolutionary aspects do not seem entirely clear and they may even be partly inconsistent with some of his main conclusions as to forces and processes in evolution.

Under "cladogenesis," which is defined as phyletic branching ("Stammverzweigung"), Rensch includes the so-called "explosive phases" or, better, "Virenzperioden" in evolution, which clearly do involve branching, but he excludes the ordinary processes of speciation in the sense of separation of two (or more) populations by an isolating mechanism. Yet speciation, in this sense, is certainly also phyletic branching and it is indeed (in my opinion and I believe also in Rensch's) the *only* way in which such branching occurs. The further divergence of the various branches after the speciational separation occurs is hardly itself an aspect of branching, even though diversification within each group may continue by continued branching.

Rensch moreover includes and emphasizes under "cladogenesis" the various phenomena involved in progressive specialization and, particularly, the origin of new organs and new basic structural types or "Baupläne." Now, it would appear that this is not correctly conceived as an aspect of cladogenesis, "Stammverzweigung," unless the new organ or new basic type (and hence a new higher taxonomic category) appeared at the time of the branching, as a phenomenon of the branching itself and not as a progressive development within a continuous line of descent. This view is supported by Schindewolf (see below), but Rensch takes particular pains to confute Schindewolf's thesis. Rensch evidently believes (as do I) that a line eventually destined to develop a new basic structural plan or to progress and diversify into a major taxonomic group begins, first branches or separates, by ordinary processes of speciation, or "intraspecific evolution." Rensch's distinction of such an event from speciation thus seems confusing and contradictory not merely in terminology but also in concept.

Rensch also insistently points out (and again I heartily concur) that the actual development of the new structural plan is a gradual process, and this occurs either after the group has branched off or progressively in a continuous line in which branching is irrelevant. His consideration of this, as well as of specialization, as an aspect of cladogenesis thus, again, seems confusing and introduces conceptual difficulties as between cladogenesis, "Stammverzweigung," and anagenesis, "Höherentwicklung." In general, anagenesis is considered as progressive change in structures and groups already established as such (similar to what I have called "phyletic evolution"), and yet the distinction from progressive specialization or from progressive development of new groups is far from clear (to me, at least), and indeed Rensch has given nearly identical examples (e.g. rise of mammals and their basic structures from reptiles and theirs) for both cladogenesis and anagenesis.

The apparent conceptual confusion involved here may be related to the difference in approach between the paleozoologist and the neozoologist. Neozoologists, with their attention focused on a single, transverse section of the life-stream, tend to think primarily in terms of simultaneous differentiation, of the separation of groups and the inception of this. Many seem to treat evolution as if it were synonymous with speciation. Paleozoologists, on the other hand, are more likely to see the problems of continuity, in the time dimension, and the rise of new categories, from the species upward, by change in time, without branching, or with branching, although present, essentially irrelevant to the basic problem. Hence some phenomena related by Rensch, as a neozoologist, to the branching concept, "cladogenesis," seem to a paleozoologist inappropriately analyzed. The distinction is one that is clearly tending to impede fully common understanding and successful total synthesis among (neo-) systematics, population genetics, and paleontology.

This analytical problem is important, but it does not detract from appreciation of still more important features of Rensch's discussion. The

very fact that Rensch does emphasize a distinction between "Stammverzweigung" and "Höherentwicklung" indicates attention to the time dimension and grappling with the whole complex of problems that involve more than the speciational aspects of evolution. In this way, Rensch encounters questions essentially paleontological in nature and does promote a synthesis between the paleo- and neo-data that is particularly helpful because it is unusual for this to come from the "neo-" side. Rensch has compiled many paleontological data, for instance in his treatment of "Virenzperioden" and, as appropriate, throughout the book. The details are often inadequate and occasionally wrong—Rensch is not a paleontologist and he had little access to recent literature in this field—yet he shows extraordinary insight in their use and he more soundly interprets their general trends than do most students with better access to details. This part of his work is especially commended to paleontologists as an example of how not merely to gather but also to understand the facts of their subject.

It is in these parts of his discussion that Rensch most nearly parallels the conclusions of my earlier work, unknown to him when he wrote this book. His evidence and examples are generally different and the approach is different, adding immeasurably to the extent of the discussion and to its integration with non-paleontological systematics, but we usually agree, often point for point, on the basic problems of these evolutionary forces and phenomena. As he notes in his addendum, this parallel is closer than is the parallel with Huxley's book or Mayr's, because the latter were little concerned with the longer time sequences and were especially interested in speciation.

Through all its great wealth of detail and consideration of special aspects of evolution, Rensch's book is a tract against autogenetic theories, which maintain that the main orienting factors in evolution are internal, not involving natural selection, and especially against the views of many German paleontologists, outstanding among whom is Schindewolf (see below). As alternative to these he supports random mutation and selection as the most essential forces in evolution. The over-simplification involved in so brief a designation of the theory is corrected by the extended treatment of the interplay of these and also of other factors in various particular phases of evolution. Rensch concludes that as between autogenesis and ectogenesis, internal versus environmental orientation of evolution, evolution is ectogenetic. Yet the regularities of evolution seem to him to be inadequately designated as ectogenetic and to be the outcome of intricate causal complexes that are preferably termed "bionomogenesis," development of the laws or regularities of life. (I would here agree somewhat more nearly with Zimmermann, as below, in holding that the alternative of autogenetic vs. ectogenetic is essentially spurious; evolution is both or, strictly, neither.)

Rensch's book closes with a rather long (more than forty close-set pages) discussion of the evolution of the phenomena of consciousness or apperception ("Bewusstseinserscheinungen"), based largely on Th. Ziehen's theory of cognition ("Erkenntnistheorie"). As nearly as I can briefly sum up an extremely complex and difficult exposition, the main idea is that the evolution of what is perceived, essentially somatic evolution in biology, proceeds in a thoroughly causalistic way, by bionomogenesis, and that at the same time and with equal universality there is a parallel, acausal evolution of perception and associated components, cognition, emotion, will, etc. This is not, however, considered a dualistic distinction of the material and the immaterial, soma and psyche, body and soul, etc. There is no separate material world, as distinct from the perceived world. The basic philosophical position is a rather subtle variety of idealistic monism.

To this point, Rensch's broader aims and philosophical positions have been stressed in this review. It is desirable, however, to emphasize that these matters do not form the bulk of his volume. His book is particularly noteworthy for an extraordinary richness of pertinent examples and for clearly reasoned interpretation of these in terms of particular evolutionary processes. The work is so packed with well-integrated information that summary is impossible and review of this aspect can be abbreviated to saying, "Well done!" and to urging any serious student of evolution to study the book. The extensive documentation and the orientation of this into a modern and mature theoretical structure will for most readers constitute the essential part of Rensch's study, and from this point of view it is fair to say that his book is incomparably more important than either of the two other publications here under review.

Zimmermann's book begins much as Rensch's ends, with a discussion of the fundamental philosophical viewpoint. Absolute contrast of induction and deduction in science is misleading. It may surely be questioned whether any scientist ever usefully gathered facts without some theoretical framework or expectation as to subsequent "induction," or whether any ever envisioned a generalization without any regard for particularities later to be "deduced" from it. Yet there are different approaches or habits of mind which tend to be inductive more than deductive, or the reverse, and these are well illustrated by Rensch and Zimmermann. Not only in his book here under review, but also through the sequence of much of his career,

Rensch has tended to move from the particular to the general. From detailed observations of local bird populations, he has inductively proceeded to ever broader aspects of evolutionary theory and higher levels of abstraction until he here faces the final query as to the ultimate nature of life and of the universe.

In his present book (I am unfortunately ignorant of his earlier work), Zimmermann's approach is deductive. He starts with generalization as to philosophical attitude, scientific methods, and their broader applications, which comprise over half his book, and then proceeds from these to rather minimal particularization. These particulars, partly by way of illustration and partly by way of ultimate test of the validity of the deductions, relate in large part to a single species of plant (*Anemone pulsatilla*). This procedure, so different from that of Rensch or of most other modern students of evolution, makes it all the more extraordinary that Zimmermann's views do converge so closely toward those of Rensch and of most western students.

Like Rensch, Zimmermann seems to be essentially a monist, but while Rensch explicitly professes idealistic monism, Zimmermann is mercilessly opposed to purely idealistic concepts and does admit a qualified dualism. He finds the contrast of mind and matter largely meaningless, because they are only different aspects of precisely the same thing. (In passing, this view is hardly distinguishable from that of most modern materialistic monists, but Zimmermann seems to imply that the "materialistic" label necessarily involves recognition also of a separate non-material and hence is dualistic.) The basic method of cognition in most fields of science (some exceptions are made) is, however, separation of the objective from the subjective ("Objekt/Subjekt-Scheidung"). This distinction leads to a sort of dualism, but one that is "consequential" on a basic monism.

On this basis, plus an axiomatic definition of "truth," Zimmermann proposes to develop a true science of evolution, which he defines as synonymous with "phylogeny." Within this field, the most important and fundamental principle is that the only objective, nature-given relationship between organisms is that of physical descent. This descent is a cyclic continuum of ontogenies. Change in successive ontogenies in the course of time is phylogeny=evolution. The whole process of ontogeny and phylogeny, which together constitute a properly indivisible unit, is given the name "hologeny."

In turning to causal analysis of evolution, Zimmermann first insists that we should not speak of "causes," "forces," or "mechanisms," but of "factors," 'factor-complexes," or, at any given moment, of the "factor-constellation."

At this point, if not before, some readers of Zimmermann's book or of this review of it are likely to exclaim impatiently, "What does that *matter!*" The "Objekt/Subjekt-Scheidung," which Zimmermann plainly considers his great contribution to scientific method, may easily seem merely banal to anyone brought up with the idea that science should be as objective as possible—and we all are, are we not? "Hologeny" for what most of us call "phylogeny," "phylogeny" for what most of us (and Zimmermann, too) call "evolution," and "factor" for what many of us call "force" and some of us call "cause"—these may seem simply playing with words. There is some basis for such criticism, and yet it is too harsh.

Zimmermann's insistence on the "Objekt/Subjekt-Scheidung" implements a slashing and (it seems to me) valid and conclusive attack on pre-evolutionary biological idealism, now recrudescent in Europe in the form of idealistic morphology or comparative anatomy. Non-evolutionary in essence, this idealistic school has strongly affected evolutionary theory, for instance overtly in the work of Schindewolf and covertly in ways more subtle and more widespread. Insistence on "Objekt/Subjekt-Scheidung" and its logical application whenever possible are means of doing more than lip-service to objectivity. This might, for instance, have put a useful end to an inconclusive recent quarrel in the United States about the meaning of homology, in which all sides claimed they were being objective, and none were in full reality.

"Hologeny" is only a word (its author favors nominalism), perhaps an unnecessary one, and the accompanying concept is not an objective reality in itself (he strongly opposes the idealistic view of reality of concepts), but it does help to bring a reality into clearer view. It helps to keep in mind that evolution is a continuous life process and that it is ontogenies, as a whole, that change—facts that many of us accept but that are not always in mind and that have implications more clearly grasped from this viewpoint. Similarly, "factor-constellation," instead of "cause," emphasizes that it is the total life situation at each moment that produces that of the next moment, and that causes of change are not separate little machines one of which can be patted on the back as *the* essential cause (like environment for a neo-Lamarckian, selection for a neo-Darwinian, or catastrophic mutation for a "typostrophist").

Like Rensch, Zimmermann is concerned with testing the autogenetic theories of evolution (although Zimmermann does not use this term for them), and he comes to the same conclusion: that they are invalid. His quite different approach and different sorts of evidence and argument add impressively to the weight of this conclusion. Zimmermann devotes even more attention than Rensch to disproof of macro-evolution (his "Makrophylogenie") and macro-

mutation, as something quite distinct in kind from microevolution and -mutation. He comes out, with Rensch, at the conclusion that the main element in evolution is interplay of selection and mutation, emphasizing still more clearly that these are not, singly or together, effective total causes but elements in a complex, analyzable but essentially unified process.

Zimmermann's analysis of details is less satisfactory, less complete, and even rather outdated. His conception of natural selection is of a "struggle for existence," with death or survival as its outcome, supplemented by sexual selection, social selection, etc. As I have elsewhere insisted, the population-genetics concept of selection, briefly that of change in gene frequencies and genomes in populations produced by differential reproduction, is distinctly non-Darwinian, so that "neo-Darwinian" for the modern synthesis is a confusing misnomer. Zimmermann is more truly neo-Darwinian or, flatly, Darwinian in many of his views. Had he been able to acquire better acquaintance with recent genetical studies, he would have seen that his various different selective factors are indeed only a few special cases of a single, far broader factor complex.

To both Rensch and Zimmermann, Schindewolf leads or typifies recent paleontological thought on evolutionary theory. Zoologist and botanist, both react strongly against the findings of (German) paleontology in this field. Rensch proceeds to analyze paleontological data for himself and to find support in them for opposition to Schindewolf and other German paleontologists. Zimmermann does this to less extent, for fossil plants, but his reaction is rather to reject or minimize the value of paleontology for evolutionary theory.

Schindewolf has not, to my knowledge, produced a recent, full account of his views. The details are scattered in many short papers, and a comprehensive summary was printed in a Hungarian journal in 1945. This review relates particularly to that publication, although several other recent papers have also reached this country and have been read as background for review of the more general account. The reader will quickly observe that I am as strongly opposed to Schindewolf's theory as are Rensch and Zimmermann, and should therefore consider this discussion as an opinion on the theory rather than as an unbiased account of it.

Schindewolf holds that the population-genetics theory of Timoféeff-Ressovsky (essentially the modern synthetic theory) accounts only for evolution within species. The origin of species and of any higher taxonomic category is, on the other hand, considered as due in each instance to a single, instantaneous mutation, a process called "Typostrophismus." The effect depends on the particular time in ontogeny at which the mutation acts. If late in ontogeny, the effect is slight and a new species arises. If early in ontogeny, the effect is great and a new class or phylum appears. It has been represented by others (e.g., by Davis, in press) that this view is reconcilable with genetical-selection theory, being merely a matter of nature and "size" of mutations on which selection has to act, but Schindewolf, himself, makes it clear that this is not his thought. The problem in selection is the spread of mutations through populations and their integration into functional genetic systems. It has been demonstrated that the chance of spread is inverse to the "size" of mutation. For a single mutation from one class to another (say for a bird hatched from a reptile's egg—and Schindewolf does give this example quite literally), the chance would seem to be effectively nil. Schindewolf also postulates a one-gene difference in the origin of all categories from species to phylum. Almost all geneticists will doubtless agree that the facts simply do not fit this postulate.

In support of this view, Schindewolf argues that the origin of new types of structure is random and not influenced by selection. (In passing, as regards many, usually minor, structures or trends, note that the modern theory attacked by Schindewolf does not demand, or suppose, that these are always adaptive or oriented by selection.) The evidence adduced for this argument is all highly inconclusive and much is flatly illogical. Each "type" is said to be a closed system; their adaptive zones do not overlap and therefore they cannot have arisen by selection.—In fact, types *beginning* to diverge do overlap, and many examples are known; in well-established, distinct types the elimination of overlapping is precisely what selection would accomplish. The first representatives of a new "type" (a phylum, class, order, etc.) are said to be undifferentiated and still devoid of any special adaptations.—Surely such a monster could not live five minutes, and certainly none has ever been seen, living or dead. If selection acted as between basic types, Schindewolf says that we would not have older basic types surviving, no protozoans and mammals at the same time. The intended implication is almost fantastically false; divergence, influenced by selection, does not always involve competition and tends precisely to eliminate this when it does occur.—This does not and obviously could not mean elimination of all diverging *lines* of evolution so that only one species of animal ever occurred on earth at any one time!

Special concern is felt for Schindewolf's paleontological evidence and interpretation of the fossil record, not only because this is his own field (and one in which he has demonstrated high competence) but also because his

views are taken by Rensch, Zimmermann, and others as the authoritative word of paleontology. From his conceptions of the fossil record, Schindewolf develops two main themes, which are interwoven in his general theory but which are not altogether dependent on each other: periodicity of development and saltatory origin of higher categories.

Schindewolf maintains that all groups of organisms develop in a three-phase cyclical manner, which is complex in the sense of having wheels-within-wheels, but which represents a simple, universal, and highly regular pattern. The postulated phases are (1) "typogenesis," a short phase of "explosive" diversification, (2) "typostasis," a long phase of progressive development without change in basic structural plan, and (3) "typolysis," a shorter phase of degeneration, overspecialization, excessive growth, etc., followed by extinction. I believe that all paleontologists agree that there are aspects of evolution corresponding roughly with the first two of these phases. Many also agree as to the last, although I do not (not, at least, without so many qualifications as to change the concept quite radically). As to their invariable sequence and cyclical regularity, however, the facts flatly do not warrant Schindewolf's generalization. His pattern is idealistic and it is imposed on data in which it is not objectively present.

N. D. Newell and I are currently engaged in gathering and analyzing very extensive numerical data bearing on these points. It is evident in these data that "typolysis" is dubious or non-existent as such, while "typogenesis" and "typostasis," or phenomena more or less like these (we reject the terms with their idealistic and saltation-theory connotations), when recognizable, occur with the greatest irregularity as to sequence, duration, repetition, etc. Still less do we find objective support for the view that "typogenesis" is in essence explosive or saltatory. A phase of intensified diversification may and often does extend over tens of millions of years, and it may occur early, middle, or late, once, twice, or more, in the history of a basic "type."

The saltatory appearance of a higher category is virtually impossible of either absolute proof or disproof from the fossil record, alone, although considerable evidence as to its probability or improbability is provided. (I discussed some of this in Simpson, 1944.) Schindewolf claims, however, to have produced an example in which this is proved, in which incompleteness of the fossil record can *certainly* (sic!—"mit Sicherheit") be excluded: the origin of the equid foot, more broadly, of the horse family. The argument is this: (1) Eohippus [*Hyracotherium*] arose from *Tetraclaenodon*. (2) They are of almost the same age. (3) The difference is greater than from eohippus to *Equus*. (4) No intermediates are known although they would be known had they existed. Therefore no transition existed; the change was "sprunghaft, überganglos."

The greatest respect for Schindewolf's ability cannot evade the regretful conclusion that in this particular argument he has been careless, to say the least. The situation regarding Schindewolf's four points (not so numbered by him) seems to me to be as follows:

(1) No student of the original materials believes that eohippus arose from *Tetraclaenodon*. If not impossible, this is at least extremely improbable. Descent from *Tetraclaenodon* (approximate, at least) is known through a series of *transitions* to *Phenacodus*, a contemporary of eohippus and quite distinct from the latter.

(2) *Tetraclaenodon* is a middle Paleocene genus; eohippus is early Eocene. The interval is on the order of 5,000,000 years, certainly time enough for a transitional sequence had one been derived from the other.

(3) The extreme improbability that eohippus did arise from *Tetraclaenodon* makes this point partly irrelevant, but not wholly so. The important point remains that, whatever the origin of eohippus, it is claimed that it represents a basic type (in the idealistic comparative anatomical sense, or a "morphotype") distinct from that of *Tetraclaenodon*, which belongs to a different order of mammals, while eohippus and *Equus* belong to the same family and, in a fairly restricted sense, are taken as having the same "type." *Tetraclaenodon* had padded, digitigrade, five-toed feet. Eohippus, which probably did have an ancestor essentially similar to *Tetraclaenodon* in these characteristics, had padded, digitigrade, four- and three-toed feet. *Equus* has non-padded, unguligrade, one-toed feet with, furthermore, a remarkable digital springing mechanism quite unlike anything in the eohippus or *Tetraclaenodon* feet. All three share many characters, such as being mesaxonic. I feel sure that any objective consideration of the actual specimens, *without regard for known intermediates*, would convince anyone that eohippus and *Tetraclaenodon* are much more similar than are eohippus and *Equus* in basic foot structure and mechanics. In other words there is more difference in "type" within the family Equidae than between the orders Condylarthra and Perissodactyla. This would certainly be recognized by the typologists were it not for the, from this point of view, quite irrelevant fact that the transition from eohippus to *Equus* is known. The "morphotypes" and the supposed "typostrophism" are wholly unnatural concepts arising from mere chances of discovery and the artifices of classification.

(4) A fairly complete transition from eohippus to *Equus* is known because much or all of

this evolution occurred in a region where a good sequence of fosilliferous continental rocks is still preserved and well-exposed and has been very intensively explored. Even if *Tetraclaenodon* had been ancestral to eohippus, there would be a long gap (late Paleocene) in the record. The record *is* incomplete, on *any* interpretation of the possible phylogeny. In fact, the only reasonable interpretation, on present evidence, is that the real ancestors of eohippus lived in some other region, where no rocks of appropriate age and character are now exposed at the surface or where exploration is inadequate—there are many such regions. Schindewolf's claim that because post-Paleocene horses are rather well known, Paleocene horses would be known if they had existed reveals striking misunderstanding of collecting conditions and of our (relatively very poor) knowledge of the Paleocene of the world.

All three of our authors are concerned directly or indirectly (in the case of Rensch) with the concept of "type" in the special sense given this word by the idealistic school of comparative anatomy. The concept has been explained for non-German readers in a clear review by Zangerl (1948), based mainly on the work of Kälin and Naef. (Incidentally, neither Schindewolf nor Zimmermann, in extensive discussions of precisely this topic, mentions either Kälin or Naef; Rensch refers to one study by Naef, but in a different connection, and he does not mention Kälin.) For Zimmermann, the concept is eliminated from serious scientific consideration by application of the "Objekt/Subjekt-Scheidung." Although he is an avowed idealist, Rensch avoids direct consideration of this quintessentially idealistic concept. For "Typus" he substitutes "Bauplan," and he argues at length and most convincingly for the gradual, selection-guided origin of "Baupläne." Schindewolf gives a favorable résumé of the idealistic morphotype concept, notes that it has been criticized as an artifact of thought (by Gross, Schuster, and Heberer, among others), but concludes that "it is, rather, the product and the expression of a wholly concrete, highly real phylogenetic event," that is, of the saltatory origin of "types."

To us American students of evolution (to mention no others), discussions such as this are often extraordinarily difficult, and sometimes completely bewildering. This applies still more to such discussions as those of Rensch and Zimmermann on theories of cognition and even more fundamental philosophical problems. We should find these helpful. It is hardly necessary to accept any particular one of these views—to me, for instance, it came as a really unpleasant shock to find Rensch avowing himself an idealist after a long discussion of evolution that could be endorsed, word for word, by the most rigid materialist—but we should realize more fully that these are problems that do concern us and our work. Almost all of us share with Rensch a basically inductive approach to evolution. We are concerned, first of all, with "getting the facts." This is excellent. It seems to me surely the best approach. But having obtained the facts, or what we believe to be facts, almost none of us make sufficient scientific use of them. We seldom carry induction from them beyond the most elementary level of theory. The three works here reviewed are all welcome for the facts (observations) that they contain, but they should all be still more welcome, in their diversity, for showing different ways of dealing with those facts and of carrying observation to higher levels of meaning.

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EVOLUTION IN *CREPIS*

EVOLUTIONARY PATTERNS IN THE GENUS CREPIS

JENS CLAUSEN

During the last thirty years the genus *Crepis*, the hawk's-beard of the sunflower family, has been the subject of one of the most intense investigations in modern biology. This program, which made the Division of Genetics of the University of California a mecca for evolutionists of many lands, was guided by Ernest Brown Babcock, for thirty-four years the head of that Division, and from 1925 to 1937 also a Research Associate of the Carnegie Institution of Washington. The results of these investigations have now been collected into a comprehensive monograph published as volumes 21 and 22 of the University of California Publications in Botany.* This monumental undertaking, which added cytological and genetical research to the traditional approaches on the study of relationships in plants, was started in 1915 and carried out by Babcock aided at various times by some 26 associates and students, many of whom came from distant parts of the world to work with him. Babcock acknowledges also the stimulating influence of his close friend, the late Harvey Monroe Hall of the Carnegie Institution of Washington, by dedicating this monograph to his memory.

The *Crepis* investigations furnish an interesting example of the evolution of a scientific program, for, following the promising lead of *Drosophila*, they were started as a purely genetic investigation of a plant group having a low chromosome number. H. O. Juel in 1905 had shown that *Crepis tectorum* had only 4 pairs of chromosomes; O. Rosenberg in 1909 confirmed this and found that *C. capillaris* had only 3 pairs. Starting with these common weeds of Europe, Babcock and his associates set out to analyze the *Crepis* species genetically, and in so doing discovered a bonanza for experimental studies on evolution. Only part of the rich strike has as yet been mined, but the investigations have progressed far enough so that the evolutionary patterns in this remarkable genus can now be ascertained.

Babcock now presents his gleanings from this mine in the present two attractive volumes. An immense amount of information has been brought together concerning the 196 species of the genus, 33 of which are described as new. The present essay will attempt to bring into focus the evolutionary highlights of this monograph and the host of technical papers that preceded it, which bulk larger than the monograph itself.

The center of distribution of *Crepis* is in the Mediterranean region and western Asia, where there are 103 species. Northern and central Europe and North America have only 11 species each, eastern Asia has 39, and tropical to south Africa has 32 species.

The 196 species are placed in 27 sections, but superimposed on this classification is a division of the species into primitive, intermediate and advanced. There is no table for easy reference where the primitive or advanced characters are listed, or where the reasons are given why they are so considered. Much of the discussion on phylogeny, distribution and migration is based on the classification into primitive and advanced species. Those readers who may disagree as to the basis for this classification will therefore find it difficult to sift fact from hypothesis in the chapters on phylogeny and migration.

The chromosome numbers of some 113 species were determined with the following result:

$n=$	3	4	5	6	7	8..11..20	
No. of species	3	58	19	14	3	3	10	3 (Total 113)

Characteristic is the preponderance of species with the low numbers of 4 and 5 pairs, and the rarity of polyploidy. The species with 11 as the basic number are all in North America and are probably amphiploids. All the 6-paired species have relatively undifferentiated chromosomes, and probably are not polyploids. For the practical use of the monograph, it would have been very helpful to have listed in part one all chromosome numbers determined and to have included the excellent drawings of chromosome morphology of all the 113 species arranged by sections, as in Babcock and Jenkins' report of 1943. It is necessary to have this paper available in order to study the *Crepis* monograph intelligently.

One of the most characteristic features of *Crepis* is its overwhelming number of endemics. Babcock lists 133 of the 196 species as endemic, 48 of these having a distribution of 50 kilometers

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* Ernest Brown Babcock: The genus Crepis. University of California Press, Berkeley and Los Angeles, 1947; Cambridge University Press, London.

Part I: The taxonomy, phylogeny, distribution, and evolution of Crepis. pp. i–xii + 1–198, frontispiece, plate 1, figures 1–11 and A–D, tables 1–12. Cloth $4.00; paper $3.50.

Part II: Systematic treatment. pp. i–x + 199–1030, plates 2–36, figures 12–305, tables 13–19. Cloth $12.00; paper $10.00.

or less. This is a most unusual situation, and one expects to find, as one does, special isolating mechanisms operative within the genus in order to keep so many species distinct, many of which occur in overlapping ranges.

The *Crepis* investigations combine the time-honored morphological studies in field and herbaria with the newer experimental approach of growing plants in a uniform environment, affording the opportunity for a comparative study of genetic variation and chromosome morphology, and for extensive crossing experiments to test the genetic and cytological relationships between species and subspecies. Although this is elaborated in part one, part two also shows the influence of the experimental approach. The neat and detailed drawings of each species include diagrams of the haploid set of chromosomes whenever known. The specific diagnoses contain a reference to the chromosome number, and the discussions on relationship contain frequent references to the experimental work.

Despite these modern innovations one senses that the old and new approaches to taxonomy are not yet thoroughly coordinated, although both are represented. On the one hand, it is maintained (pp. 57–58) that "crossing experiments provide a valuable criterion for determining species relationships," on the other it is definitely stated that the classification has been based primarily on comparative morphology (p. 4), and that the *Crepis* species are not classified "on the basis of the degree of intersterility or interfertility demonstrated by interspecific crosses, as suggested by Clausen, Keck and Hiesey" (p. 39). If this is so, it would appear that Babcock's classification substantiates the tenet that sound morphological classification tends to parallel the genetic one. To avoid misunderstanding, it should be emphasized that the reviewer and his associates regard neither intersterility nor comparative morphology as exclusive criteria for relationship. On the contrary, they advocate a *coordination* of the information on comparative morphology (in which they include the number and morphology of the chromosomes), ecology, genetic and physiologic intercompatibility, and chromosome homology as a key to better founded conclusions on taxonomic and evolutionary relationships. They agree with Babcock that a system built one-sidedly on either genetics or cytology is just as unbalanced as one founded on morphology alone.

The genus *Crepis* provided inherent limitations to a fully coordinated study. It is so large that no person in his lifetime could expect to complete a fully comprehensive investigation. Babcock had to conduct his exploratory investigations in morphological taxonomy at the same time that some of his students and coworkers examined the cytology of the genus and others made the crossings. This meant that, on the one hand, the planning of the crossing experiments could not fully benefit from the slowly accruing results of the exploratory taxonomy, and, on the other, that the final taxonomic conclusions could not have all the benefits that come from a thoroughly planned and integrated genetic program.

The *Crepis* investigations were started at a time when few people used experimental methods in research on plant relationships. In the United States, Ezra Brainerd had initiated his experimental program on the relationships of the eastern stemless violets around 1904. In Sweden, N. Heribert Nilsson had published his large paper on the hybrids between willow species in 1918. Both of these early attempts were of a very exploratory kind. The *Crepis* monograph represents a transitional stage in the development of the new taxonomy. Figuratively speaking, one foot is safely planted in the time-tested morphological approach, but the other is on the still uncompleted bridge that will eventually lead to a new kind of taxonomy.

Actually, Babcock let the experimental results influence his taxonomy more than he claims credit for. In the introduction, discussing the basis for comparative morphology (p. 4), he mentions inconspicuously that two species, *Crepis pulchra* and *C. palaestina*, were originally described in monotypic genera. They were later kept in distinct sections. When it was found, however, that they have practically identical chromosomes and hybridize easily, producing a 30–50 per cent fertile F_1 and a vigorous F_2, Babcock placed them adjacent in one section. A rather similar example is afforded by the merging of the genus *Rodigia* with *Crepis* as a result of genetic evidence (p. 14).

In an earlier paper (Babcock, 1936) the members of the *Crepis vesicaria-taraxacifolia-myriocephala-hieracioides-hyemalis* complex were treated as distinct species, but in the monograph they are merged as subspecies of one species, *C. vesicaria* (pp. 825–865). This change is completely in agreement with the fertility of their hybrids and the homology of their chromosomes, although Babcock scarcely indicates that these data have influenced his decision.

A total of 195 interspecific hybrid combinations were attempted, resulting in 117 hybrids between diploid species and 13 in which one or both of the parents were polyploid. This information is briefly summarized in one large tabulation. In approximately 40 of the interspecific hybrids, the chromosome pairing has been analyzed, but the results were published earlier, in 12 papers totaling some 400 pages, which should be read in conjunction with the monograph to provide a fuller picture of the evolutionary patterns in the genus. One wishes that these valuable experimental data had been a

little more closely coordinated with the traditional morphological ones and utilized in the conclusions.

Taken as a whole, Babcock's concept of *Crepis* species meets the crossing criterion very well. The 130 interspecific hybrids are almost all partially or completely sterile. Only two notable exceptions to this rule are found. Two of the new endemic species, *Crepis Thomsonii* from Afghanistan and northwest India, and *C. eritreënsis* from Eritrea, form fully fertile hybrids between themselves in captivity and with various forms of *C. foetida*, a widespread species of central and southern Europe, extending eastward to the Caspian Sea. The three are geographically isolated but morphologically closely related and genetically intercompatible, and their chromosomes pair perfectly in the hybrids. In an evolutionary sense they have just begun to diverge from each other, and they are certainly much more closely related than most *Crepis* species. None of the six reasons listed on page 17 for keeping them as separate species appears to have real validity, because any one of these differences may also distinguish generally accepted subspecies within one species.

Many of the [present] 27 sections appear to be natural, their species being closely related morphologically, cytologically and genetically, and clearly separated from those of other sections. Some of the sections, however, appear to be artificial. The reviewer, to test the degree of genetic relationship within the genus, went to the effort of diagramming in polygons the results of a large percentage of the crossings. This method quickly discloses whether the conclusions based on morphological relationship coincide with those based on genetic relationship. One diagram included all the 66 interspecific crossings in sections 23 to 27, another the 18 within section 20, and a third the 32 intersectional crossings involving sections 4, 9, 14, 19, 20, 23, 24, 25, 26, and 27. The polygons showed that the intersectional hybrids with few exceptions were either completely sterile or nearly so, with fertilities less than 5 per cent.

The crossing polygon of sections 23 to 27 disclosed one large complex of closely related 4-paired species in section 25. It included the widespread *C. vesicaria*, the Caucasus endemic, *Marschallii*, the narrow endemics of North Africa, *Clausonis* and *Fontiana*, and the insular *canariensis*, *divaricata* and *Noronhaëa*. Genetically, these species are much more intercompatible than most other *Crepis* species, their chromosomes are homologous, and their hybrids are only moderately sterile, being largely in the 10 to 65 per cent fertility class. They are evidently distinct ecospecies of one species complex (cenospecies) in the earlier stages of differentiation. But this complex includes also a species of section 26, *amplexifolia*, which is another North African endemic of non-overlapping distribution. Cytologically, morphologically and geographically this species appears to fit as naturally in section 25 as in 26. Genetically it belongs definitely in section 25.

The experimental investigations would seem to suggest another change in classification. One of the intersectional hybrids was startlingly fertile. This is *Crepis aurea* × *leontodontoides*, both parents of which are 5-paired, but placed in sections 4 and 9 respectively. The chromosomes of *aurea* are morphologically distinct from those of the other species in its own section, but remarkably like those of *leontodontoides* of section 9 (see Babcock and Jenkins, 1943, pp. 246 and 251). Unlike the situation in most other intersectional hybrids, the pairing between the parental chromosomes of this hybrid was nearly perfect, the F_1 hybrid was vigorous, and the fertility, classified as low, was in the 10 to 25 per cent range, which is good for fairly closely related ecospecies of the same species complex. All other hybrids of *leontodontoides* and *aurea* are either highly or completely sterile, even those with species of their own sections. The distributions of these two species overlap in France and Italy, except that *aurea* is generally at a considerably higher altitude than *leontodontoides*, and *aurea* is accordingly more perennial. There is nothing in their general morphology that would appear to force these species into different sections, but on the contrary the cytological and genetical evidence indicates that they are much closer related to each other than to other species.

Interspecific hybrids with fertilities so high and chromosomes so homologous as those just discussed are not very common in *Crepis*. The cytological information accumulated by Priscilla Avery, Arne Müntzing, C. F. Poole, S. L. Emsweller, H. A. Tobgy, and Marta Sherman indicates that in the evolution of *Crepis* species, repatterning of the chromosomes has been the most common evolutionary process. Such inter- and intraspecific exchanges and inversions of parts of chromosomes has led to isolation based in the structure of the nucleus without many concomitant gross differences in external morphology. This explains not only the reticulate morphological relationship pattern uncovered by the taxonomic classification and the considerable degree of crossability between species of different sections and of low chromosome numbers, but also the characteristically different form of the chromosomes in related species and the extreme endemism. Here evolution provided an easy means for quick development of barriers to interbreeding, and the new units could exist in close proximity to each other without danger of frequent intermixing.

The repatternings and translocations make the identification of the homology of A, B, C,

D, and E chromosomes fairly illusory, because, for example, an A-chromosome of one species may contain segments of a D from another. The 4-chromosome species, *Crepis Kotschyana,* belongs to a 5-chromosome group, but lacks the E-chromosome of the others. The segments of this chromosome are, however, distributed on the A, C, and D chromosomes of *Kotschyana* (Marta Sherman, 1946).

The North American species, constituting section 15, appear to have started an evolutionary pattern of their own. They all have $n = 11$ chromosomes or multiples of that number. The only other *Crepis* species in North America are two 7-paired members of section 12. It has been suggested that the 11-chromosome species are amphiploids that arose through crossings between 7- and 4-paired ones. One widespread species of section 15, *C. runcinata,* has remained diploid with 11 pairs of chromosomes, but in addition to their restricted diploid forms the other nine have built a complicated polyploid superstructure of forms with $2n = 33$, 44, 55, 66, 77, and 88 chromosomes, some probably autoploids, others amphiploids. The higher polyploids are all largely apomictic (asexually reproducing) species. It is interesting that such an independent evolutionary pattern has arisen in a group of species so effectively isolated from the others.

A study of this unique genus reveals a remarkable multiplication of largely endemic species in the center of its distribution, these having only 4, 5, or 6 pairs of large chromosomes that differ morphologically from species to species. A few tetraploids with $n = 8$ and three octoploids with $n = 20$ evolved as ripples on this repatterning wave of speciation. Some of the species are more adaptable than others and have a wider distribution, extending the area of the genus to the north, east and south from its Mediterranean and west Asiatic center of distribution.* One emergence into central and south Africa consists of 24 species, all belonging in section 8, and all with 4 pairs of chromosomes. Another group of 4- and 5-paired species extends through the mountains of Asia. Still another, of 7-paired, high-altitude species (section 12), may have a very different origin and be related to the equally high-altitude *Ixeris alpicola* of Japan. It has species in the mountains of Asia and North America, one of these, *Crepis nana,* occurring in both continents. Species of this section are thought to have entered into the parentage of the probably amphiploid 11-paired *Crepis* species of North America and their apomictic, high polyploid derivatives.

That some species of *Crepis* have had a wider distribution in the past than at present is evidenced from plate 1 in the first volume. It illustrates the striking similarity between Pliocene and modern akenes of three species, namely, *C. terglouensis,* $n = 6$, *conyzaefolia,* $n = 4$, and *mollis,* $n = 6$. The Pliocene akenes of the former two came from southeast Holland. Neither species occurs there today, *terglouensis* being a local endemic in the Alps, and *conyzaefolia* occurring over an arc from the Pyrenees to the Carpathians and the Altai considerably south of Holland.

It will be a long time before anyone matches the monumental evolutionary research represented by the *Crepis* monograph. It will continue to remain a rich source of information for any student of the genus and of the general subjects of chromosome morphology, homology and evolution, crossability of species, geographic distribution, and the relation between American and Asiatic species. Few scientists who set out to do an investigation of this magnitude actually persevere and bring together the information which they have gleaned as has been done in this work. Professor Babcock is to be warmly congratulated on having done so.

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SPECIATION, EVOLUTIONARY TRENDS, AND DISTRIBUTION PATTERNS IN CREPIS

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When a "member of the family" approaches the monumental work of Professor Babcock on the genus *Crepis,** he does so with a vivid memory of the long hours of patient labor which the author spent at his task, of numerous stimulating discussions with him on problems of species formation, distribution, or phylogeny, and of the eagerness with which he would follow up any new "lead" which would bring him closer to his goal of understanding thoroughly the evolutionary processes which have taken place in this remarkable genus. He also remembers numerous differences of opinion in interpreting the facts of morphology and distribution. Most of these disappeared or were reduced to negligible

* Babcock, E. B. 1947. The genus *Crepis,* parts 1 and 2. University of California Publications in Botany, Volumes 21 and 22.

proportions after further study of the plants, more reading, and more profound thinking on the part of one or more often both of the discussants. Part of the present discussion may be considered as a "minority report" on points of interpretation in which the present writer still disagrees with Professor Babcock; and part will be devoted to his accustomed pastime of "sticking out his neck," and suggesting some hypotheses about the cause of the evolutionary trends in *Crepis* which the author of the monograph thought wisest to leave alone.

The first subject to be discussed is that of isolating mechanisms and the origin of species. As a medium for understanding the species-forming processes, *Crepis* has many advantages and some very important drawbacks, at least for botanists working in the United States. Its advantages are the ease with which the species can be grown and hybridized, as well as the low chromosome number and distinctive karyotypes, which make relatively easy the recognition of species barriers produced by structural changes in the chromosomes. Furthermore, since most of the species of this genus are diploid and cross-fertilized because of self-incompatibility, the worker on the Old World species of *Crepis* is not much bothered by such phenomena as polyploidy, apomixis, and self-fertilization. These, although common in the higher plants, are thought of by most students of evolution in general as abnormal situations, and therefore to be avoided if one wants to establish principles of general validity governing the origin of species. The great disadvantage of *Crepis* to any botanist not living in the Mediterranean region is that most of the species cannot readily be studied under natural conditions, and most of the information about their ecology and degree of isolation in nature must be obtained second hand.

This situation has permitted Professor Babcock and his coworkers to recognize certain isolating mechanisms, such as geographical isolation, ecological isolation, seasonal isolation, and hybrid sterility due to chromosomal differences between closely related species, as being unquestionably important in keeping apart the species of *Crepis*, but has prevented him from giving a clear picture of the interrelationships between these mechanisms. On page 147 he states that "Isolation leading to speciation may be caused by (1) *spatial separation* or (2) *an internal mechanism*." This statement could be interpreted as meaning that either of these two factors might initiate speciation, and Babcock does not state explicity in any part of his discussion whether or not he believes that internal isolating mechanisms can begin the process in a single population, i.e., in "sympatric speciation," as defined by Mayr. However, among the examples which he discusses of closely related species between which the isolating barriers have been analyzed, there are none which require sympatric speciation for their explanation, or even in which this hypothesis is the most probable one, and several which point rather clearly to spatial separation as the initial isolating mechanism. Thus in the group of *C. neglecta-fuliginosa-cretica*, discussed on page 148, both spatial isolation and hybrid sterility due to chromosomal differences serve as isolating barriers. But, as Babcock has pointed out, the most logical assumption is that they had a common ancestor which, probably at the end of the Pliocene epoch, ranged through the then continuous area which included the ranges of all three of the modern species, namely from northern Greece to Crete. But the events of the Pleistocene caused the breaking up of this ancestral population into three parts, one isolated on the island of Crete, one on the southern peninsula of Greece, and one on the northern mainland. Since the climate of this area became progressively drier from north to south, the southernmost segment of the population evolved into the most reduced, rapidly maturing species, *C. cretica*, the middle segment into *C. fuliginosa*, intermediate in this respect, and the northern one into the larger, more slowly maturing *C. neglecta*. The relation between these changes and the origin of the chromosomal differences which are known to exist between the three species is not clear, but since the fixation of such differences would take place most easily in populations of reduced size, the most plausible hypothesis is that they became established after the geographic isolation was complete.

Babcock remarks (p. 149) "that 41 per cent of the comparable species in the genus are at present geographically isolated from their closest relatives. . . ." Furthermore, study of the distributional maps of the most advanced sections in the genus, nos. 20 to 27, shows that in nearly every instance the nearest relative of a given species is found in a geographically distinct area, or the areas of the two most closely related species overlap only slightly. The most conspicuous exceptions to this rule are found in section 20, which contains the very complex species group centering about *C. foetida*. In this group three forms judged on the basis of interfertility to be subspecies of the same species, namely subspp. *typica*, *rhoaedifolia*, and *commutata* of *C. foetida*, occur together over a considerable area of Greece, Macedonia, and Asia Minor. Here, however, we find the condition of self-compatibility and autogamy, an unusual one in *Crepis*. This is almost certainly a derived condition with respect to *Crepis*, and not a primitive one, as suggested by Babcock on p. 703. Not only the primitive species of *Crepis*, but also those of all other genera of the Cichorieae are either known to be self incom-

patible or have characteristics (large, showy flower heads, variability within populations), which are normally associated with self-incompatibility and cross pollination. Self-compatibility and autogamy appear sporadically in specialized, mostly annual species of *Lactuca, Sonchus, Microseris,* and other genera. Where present, they make possible a temporary isolation between interfertile forms which occupy the same area. Since the members of the *C. foetida* group are aggressive weeds, Babcock's suggestion, that some of the subspecies were formerly better separated from each other geographically than at present, is very plausible. They may be recognizably different now only because they have been together for a relatively short time, and because the autogamy of some forms has delayed their amalgamation. Nevertheless, the extreme polymorphism present in this group suggests that considerable hybridization between different subspecies or species has taken place in the past and that, as Babcock has suggested, some of its recognizable entities are of hybrid origin. This group, more than any other, seems like one in which evolution is progressing rapidly at the present time, and in which still more intensive study will disclose various stages in the origin of species. Study of its populations in the field would be particularly desirable.

The next topic to be discussed, the phylogenetic trends which Babcock has noted in *Crepis,* is of even greater general interest than his evidence of speciation. There is ample evidence that the following characteristics are primitive:

perennial habit, flowering stalks with few branches, large involucres and florets, involucral bracts evenly imbricated and unspecialized in structure; achenes beakless and all similar in the same head;

and that the reverse conditions are advanced characteristics—annual habit, much branched flowering stalks, small involucres and florets, involucral bracts consisting of a large inner and a small outer series, inner involucral bracts thickened, achenes beaked, and dimorphic achenes.

The predominant trends in external morphology have therefore been reduction in the life cycle, reduction in size and increase in number of the reproductive parts, and specialization of the involucral bracts and achenes. These trends have taken place independently in a number of different phylogenetic lines. They have been accompanied by the following trends in the alteration of the karyotype: reduction in absolute chromosome size, reduction in chromosome number, and increasing asymmetry of the karyotype. The progressive nature of these trends, and the fact that they have been repeated independently in different lines, both suggest that they have been directed by natural selection. As Babcock has suggested, the selective agent at work has been principally the increasing desiccation of the climate, particularly the advent of a Mediterranean type of climate, with mild, wet winters and dry summers. In a plant group like the primitive species of *Crepis,* which have no characteristics preadapting them to drouth resistance, adaptation to dry conditions can be accomplished most easily by the development of the annual habit, which permits the plants to accomplish their growth during the wet season, and in fact makes them drouth-evading rather than drouth-resistant. The drier the climate and the shorter the wet season, the greater is the selective pressure for a shortened life cycle, and consequently for reduced size of the floral parts, since the smaller the parts, the more quickly they can mature. Furthermore, the change to the annual habit greatly increases the selective value of efficient means of seed dispersal, since annuals depend on seeds for their existence to a far greater extent than perennials. The thickening of the inner involucral bracts, as well as the development of beaked and dimorphic achenes, can both be regarded as adaptations for more efficient seed dispersal.

The selective value of efficient means of seed dispersal can be increased not only by the change to the annual habit of growth, but also by adaptation to pioneer habitats, such as rock ledges, talus slopes, and areas of disturbed soil. If species are adapted to stable plant associations, such as those of forests and meadows, their individuals can live for very long periods of time, and the descendants of any individual can occupy the same site as that in which their parent grew. But pioneer habitats are by definition temporary in nature, and plant species adapted to them must be able to migrate freely, so as to occupy a new site when conditions in the old one become unfavorable. Hence, other things being equal, we should expect to find that mechanisms for dispersal and establishment would be better developed in species adapted to pioneer habitats that in those adapted to stable ones. This would explain the fact that many of the tap-rooted perennial species of *Crepis,* as well as those of *Leontodon, Hypochaeris,* and similar genera of the tribe Cichorieae have already evolved specialized achenes and in some instances a high degree of differentiation of the involucre as well.

The fact that in all three of these genera the same three trends in the alteration of the karyotype have accompanied morphological specialization and reduction in the life cycle suggests that both the morphological and the cytological trends have the same selective basis. Reduction in chromosome size has been found to accompany the appearance of the annual habit in *Silene* and other genera, and it may be a by product of the

action of some types of genes which shorten the life cycle. This cannot be a universal property of such genes, however, since in the grass family many of the most reduced and rapidly maturing annual species of *Bromus, Hordeum,* and other genera nevertheless have as large chromosomes as their perennial relatives. Investigation of the inheritance of chromosome size and length of life cycle in offspring of such hybrids as *Crepis neglecta* × *fuliginosa* might yield valuable information on the relation between certain types of gene action and visible characteristics of the chromosomes.

The decrease in chromosome number and the increasing asymmetry of the karyotype must, however, have a different relationship to the evolutionary trends in external morphology, since they are already highly developed in long lived, slow growing species like *C. chrysantha, C. blattarioides,* and the species of section 8. A tentative hypothesis to explain these cytological trends is offered here; it forms part of a more general discussion of the relationship between the genetic system and the mode of life of the plant, which is being presented in a book on plant evolution, now in press. If a plant species is to become adapted to pioneer situations, whether as a perennial or an annual, it must become an "opportunist," and be able to colonize rapidly any available habitat which has the right ecological conditions. Complete panmixy, coupled with a high degree of independent assortment of genes, makes for a great amount of genetic variability, and the offspring of any individual with these characteristics may be moderately well adapted to a variety of habitats, but may be so diverse in their adaptational requirements that they cannot all colonize a single rather specialized type of habitat. For this purpose, the offspring of a plant adapted to such a specialized habitat should be relatively uniform and similar to their parent. Two ways of achieving this genetic homogeneity are by means of self-fertilization and apomixis, and both of them have been adopted by various genera found in pioneer habitats. A third way of achieving temporary homogeneity would be by increasing the amount of genetic linkage, as is explained by Babcock (p. 146). In the words of Mather, this is another way of increasing immediate fitness at the expense of long-term flexibility. Reduction in basic chromosome number would certainly increase the amount of linkage. In this connection, it is important to note that the species of *Crepis* are characterized by a remarkably low frequency of chiasma formation and therefore of crossing over. How increasing asymmetry of the karyotype could increase the amount of linkage is not evident at present, but the possibility of a connection between these two phenomena should be explored. It is possible, therefore, that both the cytological and the morphological trends which have been predominant in *Crepis* and some related genera have been governed by adaptation first to pioneer habitats and then to the annual habit of growth.

In the light of this discussion, the writer wishes to take up the question of whether the possession of a rhizome is a primitive character in *Crepis,* as Babcock has stated in his monograph, or whether it is an advanced one, as Clausen has suggested in an accompanying review article. The first points to be considered are those mentioned by Babcock in his appendix, pp. 159 and 160; namely, that the presence of a taproot is a general and undoubtedly primitive condition in the genus *Dubyaea,* the most primitive of the Cichorieae and the probable ancestor of *Crepis;* and that certain rhizomatous species of *Crepis* have taproots in their early stages of growth. This evidence supports the suggestion of Babcock, that the rhizome was developed from the taproot as an adaptation to meadow and moist woodland habitats. In the light of the discussion given above, this reviewer suggests that the acquisition of this structure and the consequent adaptation to more stable, widespread habitats has itself been responsible for slowing the rate of evolution, and particularly of specialization of the reproductive structures. The rhizomatous species are bradytelic; in the words of Simpson "they are so well adapted to a particular, continuously available environment that almost any mutation occurring in them must be disadvantageous." If the hypothesis connecting reduction in chromosome number with adaptation to pioneer habitats is correct, it is further evidence in favor of this point of view, since a number of the rhizomatous species, particularly those of section 13, have 4 pairs of chromosomes and karyotypes as specialized as those of most of the taprooted perennials. The best assumption would be that their immediate ancestors were 4-paired taprooted perennials, adapted to pioneer habitats, which were in turn descended from 5-, 6-, and 7-paired species adapted to similar habitats. Such an hypothesis would require the additional assumption that all of the most primitive 6-paired species of *Crepis* are extinct, but this does not seem improbable to the writer. If they occurred in impermanent, pioneer habitats, they could have been easily crowded out and superseded by their more efficient derivatives. This could also have been the fate of the primitive 7-paired ancestors of *Crepis.*

The final subject to be considered is that of geographic distribution and the place and time of origin of *Crepis.* Professor Babcock, in his discussion of this topic, has made one of the most thorough and stimulating reviews of the pertinent literature on plant geography that has ever appeared in a monographic study. Nevertheless, there are some points with which the

present writer wishes to take issue. The principal one concerns the reference to Matthew's principle, which Babcock aptly summarizes on page 75 as the hypothesis "that at any one time in a large group of organisms showing close phylogenetic relations the most conservative will be found farthest from the center of origin and the most advanced, nearest to the center of origin." At no time does Babcock state that the application of this principle to *Crepis* as a whole supports his hypothesis that the genus arose in the Altai-Tien Shan region of central Asia, but he does make this statement in regard to a number of the more primitive sections. And in no case does it seem to this writer that Matthew's principle as stated above points to the origin of *Crepis* as a whole or any of its larger sections in central Asia.

In regard to *Crepis* as a whole, this is particularly clear. The most advanced species in the genus are those belonging to the last nine sections, nos. 19 to 27. Study of distributional maps of these sections shows that in seven of them the largest number and the most advanced species occur in the eastern half of the Mediterranean region, from southern Italy to Egypt, Palestine, and Asia Minor, while one has its center of variability in the western Mediterranean, and only one, consisting of four species, is centered near the Altai—TienShan region. As for the most primitive species, the largest number of them is found in the Alps, which contain some species belonging to 5 out of the first 6 sections, and are the center of variability for 3 of them. The Alpine region may be considered the northern periphery of the genus with reference to the eastern Mediterranean region, since the only species found north of the Alps are a few widespread ones like *C. paludosa, C. mollis, C. biennis,* and *C. capillaris.* The western periphery is the home of the most common species of primitive section 7 as well as the center of the advanced section 25; the southern periphery, tropical Africa, is occupied by the relatively primitive section 8; while the eastern periphery with respect to the Mediterranean regions, namely central and eastern Asia, is occupied by members of four primitive sections, nos. 1, 2, 4, and 5 by various intermediate species, and by the four species of the advanced section 21. Thus the application of Matthew's principle to *Crepis* as a whole would lead directly to the assumption that this genus arose in the eastern half of the Mediterranean region.

In his further discussion, Babcock states that the distribution of the first 11 sections is consistent with Matthew's principle in pointing to the origin of *Crepis* in the Altai—TienShan region. But only three of these sections contain more than ten species, and therefore could be regarded as "a large group of organisms," and thus subject to interpretation according to Matthew's principle. These are sections 8, 10, and 11. Section 8 is almost entirely African, and according to Matthew's principle would have to be considered as having originated from some relatively undifferentiated species of the genus which became isolated on that continent in an early stage of the evolution of *Crepis.* In the very large section 10, the four most primitive species range from the Caucasus and western Persia to Turkestan, another relatively primitive one is in northern Europe, while the most advanced species occur principally in Greece, which therefore would be considered the center of origin of this section if Matthew's principle were followed. In section 11 the most primitive species are one in Bulgaria and one in central Asia, which are near the northwestern and northeastern peripheries of the section, while the most advanced species are in Armenia and Persia, which would therefore be the center of origin for this section on the basis of Matthew's principle. The only sections which, on the basis of Matthew's principle, could be assumed to have their origin in central Asia, are the five which are largely confined to that continent, nos. 2, 12, 14, 18, and 21. The largest of these is the anomalous no. 12, with seven species, and all five together include only 21 of the 196 species in the genus. Thus the application of Matthew's principle does not lead to the assumption of a central Asiatic origin for any large segment of the genus, and Babcock's reference to this principle seems to obscure rather than to clarify his discussion.

Nevertheless, the other evidence presented by Babcock which favors the hypothesis that *Crepis* originated to the north and east of its present Mediterranean center is so extensive and convincing that there is good reason from this evidence alone to question whether Matthew's principle can be applied to *Crepis.* And when we inquire into the background of this principle, we find even further reasons for questioning its application. Matthew worked out his principle on the basis of distribution patterns in fossil and recent mammals, and based it on two primary assumptions: first that the major evolutionary development of a group takes place in one region to which it is best adapted because it originated there, and second that the species migrating out from this center do so at approximately equal rates. Neither of these assumptions holds for plant groups which have been evolving over a long period of time, during which there have been extensive climatic changes. Most plants are more sensitive to climate than are mammals. There are many mammalian genera like *Felis, Bos,* and *Ursus,* which range all the way from the tropical rain forest to boreal or even arctic regions, but such genera are very rare in plants. Furthermore, evolution in mammalian lines does not often

affect specifically the ability of the species to migrate; while in many plant groups, as in *Crepis*, one of the principal evolutionary trends is the development of more efficient means of seed dispersal and therefore of migration. This means that even if we accept Matthew's cardinal assumption that evolution is likely to progress the farthest in the region to which the original members of the group were best adapted, we can apply his principle to plants only by thinking of this region as a climatic zone or province rather than a geographic area. If, therefore, we accept this necessary modification, the interpretation of the distribution pattern of *Crepis* in the light of Matthew's principle leads to the hypothesis that the genus arose in a region which had in the early part of the Tertiary period a climate similar to that now prevailing in the eastern Mediterranean. Fossil evidence indicates that such a climate did not exist in the Mediterranean region at that time. The progression of climates in the northern hemisphere since the early part of the Tertiary period has been from warmer to cooler, and from relatively insular, i.e. with even temperatures, to relatively continental, with greater and greater extremes of temperature. Hence we should expect the principal plant migrations during this period to have been from north to south, and from the interiors of the larger continents to their peripheries, with the species originally on the margins of the continents becoming extinct or persisting only as relics on oceanic islands or on the smaller land masses of the southern hemisphere. The southwestward migration of *Crepis* postulated by Babcock would be in keeping with these general climatic trends, and one can suggest that in the Oligocene epoch, when *Crepis* probably originated, climatic and ecological conditions in some of the mountain regions of central Asia were more like those now present in the Mediterranean region than were those in any other part of the Eurasian continent, although even there the resemblance may not have been very close. Whether the exact region of the Altai and Tien Shan is preferable to other parts of the continent is not firmly established by Babcock, because of the rather general and indirect nature of the evidence presented, but at least this region is one of the more likely ones for the origin of *Crepis* and other genera now concentrated in the Mediterranean region.

However, the extension of this hypothesis to the assumption made on pages 141 to 143, that 78 species, or nearly half of the genus, originated in Central Asia and migrated in their present form to regions as remote from this center as the Iberian peninsula or even the island of Madeira, is particularly difficult for this writer to believe. On the basis of the principal of geographic speciation, which, as stated above, holds very well for the modern, actively evolving species of the genus, we should assume that its original prototypes very quickly spread into all of the areas to which they were adapted, and that in doing so they must have evolved new subspecies and species, as well as adaptations to new climatic and ecological conditions. Many of the descendants of these early Tertiary migrants were very likely the progenitors of modern sections, and in reaching the eventual limits of distribution of the genus, they must have become still further diversified. Finally, the great oscillations of climate which took place during the Pliocene and Pleistocene epochs must have caused extensive speciation, even in some of the more primitive sections, since it must have caused a good deal of migration back and forth. In fact, the writer ventures to suggest that the only modern species which are very similar to their ancestors of the middle or early part of the Tertiary period are widespread ones adapted to stable habitats, such as *C. sibirica*, *C. conyzaefolia*, and *C. mollis*, and perhaps a few of the relics. Professor Babcock's conclusion as to the time and place of origin of *Crepis* is plausible and probably as near the truth as we can reach; but much more evidence is needed before anyone can safely postulate the place of origin of any except some of the more recent of the individual species.

The discussion here presented touches upon only a few of the numerous ideas developed in this remarkable monograph. It will be for a long time a great source of stimulation to students of plant distribution and evolution. From now on, familiarity with the work of Babcock on *Crepis* will be an essential requirement for those who expect to write a really modern taxonomic monograph which seeks to explain the evolution of the group under study.

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